DEC 13 1945

PROCEEDINGS

OF THE

American Philosophical Society

Held at Philadelphia for Promoting Useful Knowledge

VOLUME 89, NUMBER 4 DECEMBER 10, 1945

CONTENTS

Sir Thomas Smith (1513–1577) and the Beginnings of English Colonial Theory. DAVID BEERS QUINN 543

Removing Some of the Barriers to Crossability in Plants. ALBERT F. BLAKESLEE 561

Inheritance of Factors Involved in One Type of Heterocaryotic Vigor. B. O. DODGE, MARY B. SCHMITT, and ANITA APPEL 575

An Outline of the Theory of Atmospheric Eclipses. ZDENĚK KOPAL 590

The Numbers of Vertebrae in Primates. ADOLPH H. SCHULTZ and WILLIAM L. STRAUS, JR. 601

Exploratory Flights of Admiral Byrd (1940). ROGER HAWTHORNE 398a

THE AMERICAN PHILOSOPHICAL SOCIETY
INDEPENDENCE SQUARE
PHILADELPHIA 6

1945

COMMITTEE ON PUBLICATIONS

JACOB R. SCHRAMM, *Chairman*

WILLIAM B. DINSMOOR
LUTHER P. EISENHART
HENRY C. LANCASTER
WILLIAM E. LINGELBACH
ARTHUR D. NOCK
ERNEST M. PATTERSON
ADOLPH H. SCHULTZ
ROBERT L. SCHUYLER
GEORGE G. SIMPSON
HUGH S. TAYLOR

LUTHER P. EISENHART, *Editor*

LANCASTER PRESS, INC., LANCASTER, PA.

SIR THOMAS SMITH (1513–1577) AND THE BEGINNINGS OF ENGLISH COLONIAL THEORY

DAVID BEERS QUINN

Professor of History, University College of Swansea, University of Wales

For a summary of the following paper see the final paragraph. [Ed.]

No adequate account of the beginnings of English colonial ideas can be written until the plans and speculations of English statesmen and projectors on the colonization of Ireland between 1550 and 1580 have been thoroughly examined. This cannot be done until British archives are reopened after the war.[1] In the meantime Professor H. M. Jones in a recent paper to the Society[2] has drawn attention once more to the importance of the colonizing experiments in sixteenth century Ireland as contributing to the growth of English ideas on colonization, precedent to and parallel with the earliest projects for the settlement of North America. This paper is offered as an illustration of the ideas of one prominent Elizabethan statesman on colonial questions in relation to one of the earlier colonizing projects in Ireland.

I

The meager catalogues of official correspondence which are all the *Calendars of State Papers, Ireland* provide for the period 1550 to 1580 have obscured the fact that constant discussions of the possibility of establishing English settlements in Ireland were going on throughout these thirty years. The smallness of the actual achievements in colonization has tended to minimize their importance. Many of the principal statesmen and administrators of the period spent much time and trouble in considering problems of colonization. William Cecil, above all, was continuously concerned in the matter: Leicester, Sir Francis Knollys, Sussex, Sir Thomas Smith, Sir Henry Sidney and Sir William Fitzwilliam were also actively interested in colonization from the government's angle. Among the private speculators who had their own ideas of profit-making colonies in Ireland were Sir Richard Grenville, Sir Warham Saintleger, Sir Humphrey Gilbert, and Walter Devereux, first Earl of Essex.

Official views on colonization in Ireland were not static between 1550 and 1580 but developed in accordance with changing circumstances in Ireland, the fruits of experiment and the gradual clarification of what colonization implied. Some measure of English colonization is rather vaguely envisaged during the attempted, and partly successful, reconquest of the island between 1520 and 1547. The English government required permanent garrisons to retain conquered areas and it was gradually realized that some permanent plantation of English settlers round strong defence centers would probably be the cheapest and most stable means of effecting this aim. Between 1548 and 1556 Sir James Crofts and Sir Anthony Saintleger made some attempt to put this idea into practice by establishing small settlements round the garrisons constructed as screens for the eastern frontier of the English Pale in the Irish territories of Leix and Offaly. Under the Earl of Sussex this developed into a more elaborate attempt to build up a military frontier colony under government auspices in the newly-formed King's and Queen's Counties, and was accompanied by elaborate but unfruitful plans for a similar frontier colony beyond the northern border of the Pale in Ulster. A relatively small number of soldier settlers were

[1] The documentation of this paper in wartime has presented some difficulties. The Fitzwilliam Papers in the Carte MSS in the Bodleian Library, Oxford, are cited from (*a*) official transcripts of volumes 55 and 56 in the Public Record Office of Ireland, Dublin, and (*b*) a manuscript calendar (with modernized spelling) by Mr. Charles MacNeill of volumes 57 and 58 in the possession of the Irish MSS Commission (by special permission). The State Papers, Ireland, in the Public Record Office, London, are cited by their official number, SP 63, either from incomplete transcripts made before the originals were removed from London or from the unsatisfactory *Calendars*. The Smith patent and indenture of 1571 are cited from a late copy in the Public Record Office of Northern Ireland, Belfast. Sir Thomas Smith's letter-book, 1572 (PRO,SP 70/146) is well calendared, except for one or two items, in *Cal. S. P. Foreign, 1583, and Addenda 1547–1583.*

[2] *Proc. Amer. Philos. Soc.* **85**: 448–465, 1942.

established in King's and Queen's Counties at a high cost and a heavy wastage without achieving the expected stability since numbers were too few and Irish resistance too difficult to eradicate.

In these experiments the government's main consideration was military and comparatively little attention was paid to the problem of building up a new English society in what was, after devastating wars, virtually virgin territory. The matter was complicated by the fact that the government was continuously making attempts to pacify the Irish lords by inducing them to accept some minimum of English rule, and there was consequently considerable hesitation about embarking on colonization in any particular district until all hopes of a peaceful compromise with the native inhabitants had been exhausted.

During the decade 1565 to 1575, however, there was great activity, both on the part of government and of private speculators, in making plans for colonial settlements in Ireland on a much wider scale than anything hitherto contemplated. Much attention was paid to the problem of financing settlements and to the development of their economic life. It came to be realized that it was not sufficient if a small number of Englishmen were given a large amount of Irish land and set to exploit it with Irish labour, while at the same time they were saddled with military responsibilities to the government. Settlement, it came to be understood, must be reasonably intensive (though the exploitation of Irish labour was not excluded) and must consist of representatives of more than one English social class so that a real colony of settlement could be established. A satisfactory scheme must provide for towns and villages and the systematic development of local government. It must provide for reasonable economic outlets by the encouragement of trade in agricultural and other products. These were considerations developed in the course of much debate and they are of considerable significance for the later attempts to colonize North America.

After its experience in King's and Queen's Counties the English government was primarily concerned with the great cost which intensive colonization, undertaken directly by the government, would involve. Sir Henry Sidney, who was appointed Lord Deputy of Ireland in 1565 and whose first task was to crush the formidable resistance of Shane O'Neill in Ulster, found himself faced with the problem of what to do with the northern part of Ireland once it had been subdued. His particular contribution to the question of colonial settlement was his continuous advocacy of privately financed colonies between 1565 and 1575. He envisaged such colonies as alternatives, either to an extensive system of royal garrisons for keeping down the Irish, or to a royally financed and organized system of English settlement, the objection to both of which was their ruinous cost to the exchequer. He brought these views before Elizabeth and her advisers in the summer of 1566 when he sent Captain Humphrey Gilbert to England to expound them but his clearest exposition of the matter was given two years later in a letter to Cecil[3] in which he said:

> Nowe for the mayne of Ulster, to trewe it is that the charges wilbe intollerable for her Ma*jes*tie as I feare either to defend that Province by Souldioures, or to plante it with People at her owne charges, and yet one of these ij waies must nedes be taken before reformacion or Revenue can be loked for, And therefore in my opinion persuasion woolde[4] be used emonges the nobiletie, and principall gentlemen of England, that there might at sondrie mens charges without exhausting of the Princes particuler purse be induced here some Collany if it were to the nomber of 2000 men or more here were Roome enoughe for them, but they must be so furnished with mony, apparell, victualle, and meanes to tyll the grounde, and seede for the same, as if they should imagine to finde nothinge here but earthe, And in dede Littell els shall they finde savinge only fleshe, and some beastes for eareing of the grounde, And all these might well be planted in that tract of ground which I lefte vnder the Government of Piers and Malbie which is no part of Tiroine.[5] In which I am well assured there liveth not the 200th men[6] which there might well be nourrished.

The favourable reception which Sidney's views had at court led to a great number of projects in the following years by syndicates of private gentlemen for the colonization of various parts of Ulster and Munster. Munster projects came

---

[3] SP 63/26, 18.

[4] The meaning is "should."

[5] In October 1567 William Piers and Nicholas Malbie had received a commission to exercise martial law in the Route (in county Antrim), the Ards, Killultagh, and the Duffrin (in county Down). Piers was also seneschal of Clandeboy, covering a large part of both modern counties (*11th Report of the Deputy Keeper of the Records, Ireland*, fiants 1196, 1530).

[6] The meaning is "not the two-hundredth part of the men."

to nothing, owing to a rebellion in 1569 which lasted for several years, but after considerable government vacillation three private ventures were authorized in 1571 for the plantation of considerable parts of the modern counties of Antrim, Down, and Armagh under Thomas Smith and Captains Malbie and Chatterton. It is with that for south Antrim and east Down under Thomas Smith and his father, Sir Thomas Smith, which we are concerned below. When these projects had been given a trial and did not look like succeeding, a much bigger venture for Antrim, under Walter, Earl of Essex, was launched in 1573. This involved an admixture of royal and private control and finance, but it was never systematically pursued and its expensive failure tended to breed disillusionment in both government and unofficial circles so that before 1580 the long series of plans came to an end and was not revived until the end of the great Munster rebellion in 1583.

It is in the private projects for Irish colonies in the years 1566 to 1575 that the main interest lies for the later American ventures. Such men as Sir Richard Grenville and Sir Humphrey Gilbert became interested in projecting colonies in Ireland and this helped to turn them to America in later years and permanently coloured their ideas about colonial organisation. Both Gilbert's plans for Ulster and Munster, and Grenville's and Sir Warham Saintleger's for Munster have also this significance—they set the gentry of southwest England busily projecting the acquisition of new landed estates for themselves which later involved them deeply, alike in the earliest plans for the colonization of North America under Gilbert and Ralegh, the plantation of Munster, and the more decisive seventeenth century American ventures.

It was in the reign of Elizabeth that the age of the "projector" began. The accumulation of capital in England meant that landowners and merchants alike were on the lookout for profitable fields of investment. The younger sons of the landed gentry, too, excluded from the inheritance of landed wealth, were desperate to get riches and power by the quickest means possible. And so there appear many get-rich-quick schemes, from alchemy and piracy to colonization. The latter had one special attraction in that it could provide land—the most prized possession of all—at a time when land values in England were rising rapidly. All such schemes focussed on the court for it was the monarch alone who could give exclusive rights for the exploitation of any project. Irish colonizing projects were those most prominently under discussion between 1566 and 1575. Almost all of them—and many were quite impracticable—were ultimately dropped or discarded after official criticism, but they undoubtedly gave the first great stimulus to the discussion of the pros and cons of colonial settlement both in official and unofficial circles.

II

Sir Thomas Smith's interest in colonial settlement in Ireland is by no means surprising. He was indeed concerned with Irish matters in an official capacity, as a member of the Privy Council from 5 March 1571 and Secretary of State from 13 July 1572. His interest in colonization had, however, been roused before 1571. As a famous classical scholar he was familiar with accounts of colonization in the Roman writers. As a student of political institutions he had shown in his *De republica Anglorum*, written in 1565, a strong sense of the evolutionary nature of constitutional development, and might be expected to interest himself in the extension of sovereignty over newly-settled areas and the institutions through which this could be achieved. He was actively involved in projects for making money by new and unorthodox means, witness his connection with the Society for the New Art, an alchemical venture, between 1571 and 1576. At Cambridge he had been the tutor of Richard Eden and may even have inspired his interest in the New World. At least he was sufficiently interested in Eden to acquire two of his books. Smith's library in 1566[7] contained Eden's *Decades of the newe worlde or west India* (1555), largely translated from Peter Martyr, but with the first printed accounts of English overseas voyages, and his translation of Martin Cortez' *The art of navigation* (1561) in the introduction to which Eden paid tribute to his former teacher. Smith had at least three other works on extra-European geography, Munster's *Cosmographia*, Barros' *Asia* (1552–1563), and the French *Description d'Affrique* (1556) after Leo Africanus, along with several dozen other works on general or classical geography and topography. It is therefore clear that Sir Thomas Smith was acquainted with at

[7] John Strype, *Life of the learned Sir Thomas Smith*, 274–281, 1820. E. G. R. Taylor, *Tudor geography, 1485–1583*, 37, 193–236, 1930.

least the outlines of the European expansion of the previous century and with some of the problems of its colonial experiments.

Throughout his extremely varied career ("few Englishmen have held so many offices of such different sorts," Maitland said of him[8]), Smith had shown a restless spirit of inquiry. He had the temperament of an innovator backed by an exceptionally wide range of academic and practical knowledge. Whether it was in connection with the pronunciation of Greek, the study of the civil law, natural science or theology, the spelling of English, the history of the changes in the value of money[8a] or the date of beginning the year his restless intelligence led him to propound new theories and reforms. Perhaps it was their originality which made most of his proposals unacceptable to his contemporaries (he was in any case inclined to be rather pedantic in his approach to practical problems), but there is no doubt that he tried to apply his academic knowledge of the past to the elucidation of the present and, incidentally, to his own profit. Such a man once interested in the problems of colonization of Ireland would be certain to have valuable things to say, even though his practice was unlikely to be as striking as his theory. He was, in fact, happiest as an armchair empire builder.

III

What is clearest about Sir Thomas Smith's views on colonization is that they are strongly influenced by classical precedent. Indeed, it might be argued that it was his knowledge of ancient, and especially of Roman, history which most strongly turned his attention to the possibility of developing new English settlements on Irish land, if it were not that on his readmission to the Privy Council in 1571 Smith could scarcely have avoided the debates on Irish colonization which he found going on there. It would seem that it was the father who inspired the son with his interest in Irish land, but this need not exclude influence by the son on his father's ideas.

That his contemporaries were familiar with Roman terminology on colonies from the classical texts and did not need to derive the word "colony" from Eden's rendering of Peter Martyr's Latin of the *Decades* of 1555 is shown by Sidney's usage, in the letter of 1568 already cited, of the phrase "that there might . . . be induced here some Collany," which derives directly from the *deducere coloniam* of Caesar and Cicero.[9] But there is no doubt whatever that classical precedents had a lively influence on Smith's desire to colonize Ireland.

To Smith, the English in Ireland were the modern Romans, bringing to a savage land law, peace, and civilization. "He understands," he says in a letter to Fitzwilliam, lord deputy of Ireland,[10] "by histories how England was as uncivil as Ireland until colonies of Romans brought their laws and orders, whose moulds no nation, not even the Italians and Romans, have more straitly and truly kept."

In the preparation of a colonial programme for Ireland Smith proceeds to stress the importance of individual leadership and the exercise of personal authority by the head of an infant colony. Once more he takes his stand on Roman precedent. Roman colonies were led out into new lands by military leaders who took full powers over the colonists and full responsibility for placing the colony on a civil footing once it was securely established. So must it be in Ireland. The indenture, which was the contract between Sir Thomas and his son and the crown for the establishment of an Irish colony, promised him a commission to invade and carry on military operations in the territory granted to him. In asking Fitzwilliam to make out the commission to him and his deputy Smith asked that it should be as a "colonel." The interpretation which he put on this word caused some difficulty to the English legal officials in Ireland who knew it only as designating a commander of footmen. Twice, in 1572 and again in 1574, he argued out its interpretation from Roman precedents with Fitzwilliam.

In 1572 Smith wished his son to be, as his deputy, both civil and military governor of the projected colony. He told Fitzwilliam:[11]

[8] Preface to Smith's *De republica Anglorum*, ed. L. Alston, x, 1906.

[8a] Professor Edward Hughes shows (*Bulletin of the John Rylands Library* **21**, 167–175, 1937) that there is good reason to ascribe to Sir Thomas Smith, rather than to John Hales, the important *Discourse of the common weal of this realm of England* (ed. E. Lamond, 1893). He argues that the edition of 1581 was edited by William Smith from his uncle's MSS.

[9] See also a phrase in a letter of 6 June 1569 from Queen Elizabeth to Sidney: "touching the proceeding to the recovery of Ulster *by deducing of some Colonels* of people out of this our realm to inhabit the same . . ." (Trinity College, Dublin, MS N.1.1, no. 63).

[10] 8 Nov. 1572 (Carte MS 57, f. 435).

[11] 17 July 1572 (Carte MS 57, f. 38).

The name of a Coronel or Colonel in French is the leader of footmen, as marshal is of horsemen. Here it betokeneth a leader forth of men to inhabit and till waste and desolate places, who in ancient time were *Deductores Coloniarum*, and the action was called *deducere coloniam*. It is no name either of high honour or authority, yet wherewithal we are best content because it sheweth the nature of our actions.

Two years later, after his son's death, Sir Thomas wished to make it clear that, in the new colony he was sending out, his agent, Jerome Brett, was to have primarily military functions, while his brother, George Smith, was to distribute lands as his personal representative. On this occasion he read Fitzwilliam another lecture on "colonels":[12]

The Colonelship [is] but a name w*hi*ch riseth of the thing as I take it, not [the] governing of footemen, as some men wold think, w*hi*ch is rather Coronell, of corona, a ring or company of footemen & corruptly Colonell. The truth is that I & my deputies be in dede Coloniae ductores, the distributors of land to english men in a forein contrey, And as they who so take land be Coloni, or Coloners,[13] So we that do distribute it may be called coloniae ductores, or Colonells, a new name for an old doeng but now by me a renewed thing.

Going on to deal with the position of his brother George, Sir Thomas said:

. . . if I may apoint my deputie mareshall for defence & for warre & ponishing of offences, altho my brother be not Colonell by patent, Yet he may by my consent give away my land given to me & myne heire, to others & their heirs, vpon suche condicions as are limited, and they & he can agrea by my orders, And so in dede he shalbe Colonel, & coloniae ductor, and agrorum diuisor/Altho I onely be colonel if he in my name & for me do it.

Sir Thomas' somewhat pedantic and didactic habit of thought is apparent from these extracts yet they clarify his method of approach to Irish colonization through classical precedents. He thought of himself and his deputies as the direct successors of those Roman soldiers who had led out their colonies to extend the empire.

A final concept which Sir Thomas derived from classical analogy was that of the fortress city as a nucleus for the new society which was to be erected in barbarian lands. Before his son set out for Ireland in 1572 he sent him copious advice from France. On April 10[14] he wrote:

For the first year there, and peradventure the second, ye shall do well to take one sure and convenient place to make a fort, as Byrso was to Dido, and Mons Aventinus to Romulus, and there to fortify yourself; and that being strong and provided to live and defend may master the country about, and so the country divided into villages and parishes may make your first cottage or fort as big as any of the other was by long time and good governance.

Six weeks later Sir Thomas Smith had received from his son an outline of his ideas on the first steps to be taken on reaching Ireland: the father thereupon proceeds to lecture the son for omitting any reference to this cardinal point of a stronghold and civic nucleus. He said:[15]

But in all this, I marvel that ye have not care of one and your principal city, which I would were called *Elizabetha* . . . where it is meet that each resident have a place of ground to make his palace or chief residence, of our giving; . . . and then he to hold likewise his land and tenure of assistance, aid or patriciate of us and our heirs, by such tenure as is afore, with condition to maintain in the chief castle or citadel of the city Elizabeth, one tower, against all the Queen's Majesty's enemies. I reckon that you can do nothing till you have a strong town, as a magazine of victuals, a retreat in time of danger, and a safe place for the merchants. Mark Rome, Carthage, Venice and all other where any notable beginning hath been . . . Choose a place strong by nature for defence as a citadel, to defend the city when it shall be made, and then it may be called *Castra colonelli* or Smith's tents, for so long till it have a better name.

In these references we have the first known academic discussion of colonization by an Englishman for whom the classics provided a living parallel and inspiration. Sir Thomas' other ideas on colonial organization and settlement are best dealt with in illustration of the planning and execution of the Irish project.

IV

The story of the Smith colony in the Ards has been told in outline by the late Robert Dunlop,[16] but, though a good deal of supplementary material has come to light since 1924, it is not proposed here to give a full narrative of the colony,

[12] 31 July 1574 (Carte MS 56, f. 218)

[13] Earliest example of this word in *New English Dictionary* is 1600.

[14] *Cal. S. P. For. 1583, & Add.*, 467–468.

[15] *Ibid.*, 490–492.

[16] Sixteenth century schemes for the plantation of Ulster, *Scottish Hist. Rev.* **22**, 1924–1925.

but rather a brief framework for subsequent comment.

The first proposal for a colony in Ulster was put forward in a petition from Thomas Smith[17] and his associates to the Queen in the spring or summer of 1571.[18] The petitioners ask for a royal grant of the Ards and other lands which they offer to conquer at "theire own charges and perils" in order "to make the same civill and peopled with naturall Englishe men borne." The key-note of the project is the privately financed colonizing expedition to establish an English colony in a savage country. Money was to be found by annual levies on the eight or nine hundred adventurers it was hoped to recruit and these were to be recouped by grants of Irish land. The articulation of the colony is then sketched. After the first conquest a defence line, manned by soldier-adventurers settled along the borders, was to be established round the territory, with garrisons in "strengthes" and "watchtoures" to defend the colony. Within the area to be settled the land was to be distributed to groups of adventurers in parishes. In each of these the church was to be the first building erected and lands were to be assigned to the clergy, the parish clerk, a schoolmaster and a constable.[19]

Naturally, the scheme comprises a native policy for the subjugation of the "wild" Irish must form the justification of the scheme to the government. The Irish lords and their military forces were to be repressed or driven out, but the labouring population was to be retained to work for the colonists:

> All Irishmen . . . which commonly be called churles, that will plow the grounde and beare no kind of weapon nor armoure, shalbe gentlye entertained and for theire plowinge and laboure shalbe well rewarded with great provision that no iniurie be offered to them.

The Irish were, however, to be forbidden to wear English dress and armour and though they were to be taught the English language they were not to be eligible to purchase land, bear office, be chosen for any jury, admitted to witness any real or personal action at law, "nor be bound apprentise to any science or arte that maie indomage the Queenes Majesties subjectes hereafter." The English settlers, in fact, were to rear their colony on a basis of servile Irish labour.

The English government accepted the scheme in essentials by the indenture of 5 October 1571 and the letters patent of 16 November[20] which granted what the grantees estimated at 360,000 English acres[21] "in the great and little Ardes in Clandeboye, which lieth south to the castle called Belfast, so to the abbey or priory called Massereene, the castle called Castle Mowbray and the Castle Toome" to Sir Thomas Smith and his son. They were to hold from the crown as tenants of the earldom of Ulster, as of the manor of Carrickfergus, by one knight's fee, paying rent for all lands occupied by 29 September 1576 and losing title to those lands not occupied by 28 March 1579.

The Smiths, father and son,[22] by an intensive propaganda drive assembled some seven hundred to eight hundred adventurers at Liverpool by May 1572. By that time news of the project had alarmed the Irish whose lands it was proposed to settle and fear of widespread rebellion led the English officials in Ireland to get the Queen to hold back the expedition until July. By that time most of the adventurers had drifted away. Thomas Smith finally set out on August 30 with little more than a hundred men. Landing in county Down he was faced with armed opposition from Sir Brian MacFelim O'Neill, the ruler of the lordship of which the greater part had been granted to the Smiths, and was too weak in men and supplies to take decisive military action. The Irish took the initiative in October and destroyed the churches and monastic houses at Holywood, Bangor, Newtownards,

[17] Thomas Smith, illegitimate son of Sir Thomas, b. 1547; recognized by his father as his heir. Served as an officer in Ireland, *ca.* 1568; discharged with pension; entered service of Earl of Leicester.

[18] Hist. MSS Comm., *De l'Isle & Dudley MSS*, II: 12–15, 1935.

[19] Thus far the scheme has striking resemblances to that developed in 1582–1583 by Sir Humphrey Gilbert for his proposed North American colony, *cf. The voyages and colonising enterprises of Sir Humphrey Gilbert*, ed. D. B. Quinn, Hakluyt Soc., ser. 2, **82–83**, 1940, *passim*.

[20] Copies in Public Record Office of Northern Ireland, Belfast.

[21] 1200 ploughlands estimated to contain an average of 300 English acres. G. Hill, *Historical account of the MacDonnells of Antrim*, 409, Belfast, 1873. The ploughland was in fact a highly variable unit and this estimate is unlikely to be closely related to the true area covered by the patent.

[22] Sir Thomas had to leave England in the thick of the preparations on a special embassy to France (10 Dec. 1571); he did not return until July 1572, but kept in constant touch with developments by letter.

Movilla, and Greyabbey—the only stone buildings in the area which could provide shelter and bases for the colony. In spite of this disaster Smith managed to establish a base some miles south of Newtownards, which he called Newcastle Comber. After a hard winter, and with some desertions from his tiny force, he was able to achieve some local and temporary successes in the spring of 1573. Sir Thomas despatched several hundred reinforcements from England in March but they never reached Ireland. A much bigger colonizing scheme, headed by the Earl of Essex, for the occupation of county Antrim, was now approved and it seemed to offer the Smiths some prospect of relief from Irish pressure. They surrendered their lands north of the river Lagan to Essex and his arrival in mid-August put new hope into the tiny colony at Comber. But within two months the settlement was destroyed. Some Irishmen employed in Thomas Smith's household suddenly attacked and killed him. This was the signal for a general rising and the remaining colonists were driven to take refuge with the old-established Anglo-Irish family of Savage in the Lower Ards. A handful of settlers remained there under Denys Smith, one of the sons of Sir Thomas' brother George, but most of the survivors returned to England.

These events, with the loss of his heir and the dispersal of the colony, were a heavy blow to Sir Thomas Smith. Nevertheless, he was prepared to make a further attempt to establish a settlement. Indeed he was bound to attempt to do so, unless he was willing to renounce all claim to his Irish land. Instructions from the Queen to the Earl of Essex, dated 30 March 1574, contained the item:

> Sir Thomas Smith shall either send some force into the Ardes to strengthen such as shall inhabit in Clandeboy, or else shall be compounded withal for his interest.[23]

By this time Sir Thomas was well advanced with the preparation of a new expedition, but once again long delays ensued before some 150 men left Liverpool and Workington for the Ards in August 1574. This time the adventurers were led by George Smith, Sir Thomas' brother, who was accompanied by his three sons, and by Jerome Brett who held the military command. The colonists reestablished themselves at Newcastle Comber, and Brett was able to arrange a meeting with Sir Brian O'Neill, now pardoned for his rebellion by Essex, and to get a provisional recognition by him of the Smith title to the Ards. But in November Sir Brian was killed by Essex and this, instead of bringing peace, led to another Irish rising under Niall Faghtertach O'Neill. Once again the colonists were driven out of their settlement and took refuge in the Lower Ards. Brett alleged that he had been deserted by many of the adventurers and it is clear that he had quarrelled irrevocably with George Smith. In January 1575 Brett was established in the Savage castle of Ardkeen and was begging the lord deputy for royal troops to garrison Holywood and Newcastle Comber so that the colony could be reestablished.

This is the last we hear directly of Smith's colonists, but in April Sir Thomas asked the lord deputy to revoke all authority from Brett whom he accused of destroying all chances of reviving the colony. Smith proposed to place his venture under the Earl of Essex who, on April 26, agreed in principle to take over all Smith's lands, but the bargain was not completed and Sir Thomas then endeavoured to get the Queen to resume the lands into her own hands. He was by this time tired of the venture, but was not relieved of his obligations. A peace between Essex and Brian Faghtertach O'Neill in July looked like safeguarding the Ards from Irish incursions and colonization again appeared feasible. A few remnants of the 1574 expedition may have emerged from the Lower Ards and begun to farm the lands round Comber, but, so far as can be ascertained, Sir Thomas sent them no further aid. His health began to fail in March 1576 and he had gradually to give up his official duties. He died on 12 August 1577 and on the memorial tablet to him in Theydon Mount Church where he was buried he was described, *inter alia*, as "Ardae Australisque Claneboy in Hibernia Colonellus."[24]

Sir Thomas left his lands in Ireland to his nephew William Smith. In June 1579 William Smith landed with forty men in the Ards to make a third and final attempt at a settlement, but the Dublin officials called him to the capital before he could make any headway and refused him permission to proceed,[25] probably on the

[23] *Cal. Carew MSS, 1515–1574*, 465.

[24] C. H. & T. Cooper, *Athenae cantabrigienses* I: 372, 1858.

[25] SP 63/75, 65; 78, 66, 67 (the first two items are printed in E. Lamond, ed., *Discourse of the common weal*, lxvii–lxxii, 1893).

grounds that his uncle's patent had become void on 28 March 1579 since no permanent colony had been established.

V

The device in which the Smiths most clearly showed the originality of their approach to the question of colonization was in the issue of printed propaganda to attract subscribers and adventurers to the enterprise.

Hitherto, published propaganda for colonization in England had been small, indirect, and infrequent. Eden's translations from the continental chroniclers of Spanish and Portuguese overseas enterprise had been prefaced by rather general inducements towards their English emulators. In the *Decades* Eden's publication of narratives of the English Guinea voyages had been a rather more open indication that he believed in the value of printed publicity. There is no doubt also that the publication in 1563 of Ribaut's description of his first attempt to colonize Florida was intended as publicity for the abortive Ribaut-Stukeley enterprise of that year. Yet even here the approach is indirect. Thomas Hacket in his dedicatory epistle to Sir Martin Bowes[26] goes no further than to say:

> I cannot but amongest the rest reioyce to see the forwardnes in these late yeares of Englyshe men. For the lyke enterprises. And what good successe GOD hath gyuen them for their trauil. For albeit that such attemptes seme paynfull and harde to acheue to. yet in the ende they be most pleasaunt and profitable. As well for the enlarging of the Christian faith as the enriching of kyngdomes.

The Stukeley fiasco had brought colonizing ventures into a disrepute which lasted at least a decade. Sir Thomas Smith said of his son in 1573:[27]

> I had rather he should adventure his lief/ then that we both should be accomptid deceivers of men, and enterprysors of Stewelies voiage of terra florida, or a lottarye as som evile tongues did terme it.

The published propaganda for the Smiths' Irish project consisted of three separate items. The earliest in point of time was probably the broadsheet entitled *The offer and order giuen forthe by Sir Thomas Smyth, Knighte, and Thomas Smyth, his sonne, vnto suche as be willing to accompanie the sayd Thomas Smyth, the sonne, in his voyage for the inhabiting some partes of the North of Irelande.* The only surviving copy is signed by Thomas Smith.[28] Published as soon as possible after the grant of the patent of 16 November 1571, this is a straight-forward appeal for subscriptions, setting out what lands adventurers would receive for specified contributions towards the enterprise. The second is more elaborate and less direct. It is a sixty-three-page pamphlet[29] ostensibly in the form of a letter from one friend of Thomas Smith to another in order to dispel doubts and criticisms which are said to have been raised about the project. In reality it is a skilfully written boost for colonization in general and for the Ards venture in particular. As such it is the first piece of sustained argument for colonization to be published in England, and it deserves more attention for its significance in the development of colonial ideas than has been accorded it hitherto.[30] *The offer and order* is reprinted at the end of the *Letter* on the pretext that it had just been received by the alleged author from Thomas Smith. The third printed item was a map of the Ards and the surrounding districts,[31] which was presumably handed to likely subscribers.

The Queen described the "book," i. e. the

---

[26] Jean Ribaut, *The whole & true discouerye of Terra Florida*, ed. J. T. Connor, *Pub. Florida State Hist. Soc.*, no. 7, 1927: a facsimile reprint of the unique copy of the 1563 edition containing the epistle.

[27] Smith to Fitzwilliam, 27 Apr. 1573 (Carte MS 56, f. 57).

[28] In the possession of the Society of Antiquaries London: see R. Steele, *Tudor and Stuart proclamations*, II, no. 73, 1910.

[29] *A letter sent by I. B. gentleman vnto his very frende mayster R. C. esquire, wherin is conteined a large discourse of the peopling and inhabiting the cuntrie called the Ardes . . .* London, Henry Binneman for Anthony K[itson] [1571]: reprinted in Hill, *op. cit.*, 405–415. It is A. W. Pollard and G. R. Redgrave, edd., *Short-title catalogue of books printed in England* [etc.], *1475–1640*, no. 1048, 1926: additional copies are in Trinity College, Dublin, and National Library of Ireland. A new edition, correcting Hill, is required.

[30] Professor H. M. Jones calls welcome attention to it in his paper previously referred to. *Proc. Amer. Philos. Soc.* **85**: 455, 1942.

[31] Printed by Henry Binneman. The only copy located is British Museum, Harleian MS 5938, no. 129. This formed the basis for the map in Strype, *Sir Thomas Smith*, facing p. 131, Oxford, 1820. It probably influenced the map of Ireland, published by Ortelius in *Theatrum orbis terrarum*, Antwerp, 1574, which bears, opposite the Ards peninsula, the legend "Hanc insulae partem Anglis incolendam dedit Elizabetha Angliae regina; Coloniaque ducta est Domino Smetho equite aurato 1572." This gave the venture a European currency.

Letter, as "set forth by the means of Sir Thomas Smith,"[32] and Sir Thomas' letters clearly show that the ideas set out in it were his own, even though the final draft was probably the work of his son. But the fact that, in the first place, the pamphlet was published without royal authority or approval,[33] and, in the second, that copies of it came into the hands of Sir Brian O'Neill and brought bitter protests from him and sympathetic echoes from the English officials in Ireland,[34] led Sir Thomas to attempt to repudiate personal responsibility for it. "The little book which my son sent out was evil done," Sir Thomas wrote to Burghley[35] once trouble had developed. Yet even then he gave a reasoned account of the pamphlet's purpose:

> I did not like of it at the first myself, as my son can tell, but when I considered that without some such admonitions and proffer he had no authority to call other, and neither he nor I had tenants or great countries of our own, to gather such a number together as was necessary, I perceived his device was not amiss, with persuasions and offer of participation of profit and honour, to allure to him whom he could, and whose hearts had some fire of life to be kindled there with them, to set to this enterprise and desire of glory.

In an apologia to the English Privy Council[36] on the same theme he was more forthright, saying:

> If any be offended by my son's books, I pray you to understand, neither he nor I had lands or tenants enough to compel to it, nor authority to muster any man; so nothing was left but persuasion, either by words or writing and writing goes further. There has been peradventure, some youthful courage not unfit for that age; the which if it has not been showed, who will follow a discouraged and coward captain.

In the words "and writing goes further" Sir Thomas Smith showed an intelligent appreciation of the value of printed publicity, and indeed the passages cited are an interesting comment on the basis of advertising. The success of his son in assembling some eight hundred adventurers within six months of the appearance of the pamphlet seems to point to its effectiveness. In any event the broadsheet, the pamphlet and the map are the first printed publicity for an English colonial project[37] and were the ancestors of a long line of similar advertisements down to our own century.

VI

The official reasons for sponsoring the enterprise are best given in the indenture of 5 October 1571 between the Queen and the Smiths. It stated in its preamble:[38]

> whereas there be within her highness' earldom of Ulster . . . divers parts or parcels that lieth waste or else inhabited with a wicked, barbarous and uncivil people, some Scottish and some wild Irish, such as late were rebellious to her highness and commonly are out of all good order and as yet were in continual rebellion to her majesty, considering how great a benefit it should be to her realm of Ireland, honour and commodity to her majesty . . . to have the same peopled with good and obedient subjects, which should acknowledge the great benefit of God, her highness' royal authority, and be of force at all times to her majesty's deputy or other officers to repress all rebels and seditious people and be an occasion by their example to bring the ruse and barbarous nation of the wild Irish to more civility of manner, have often desired and wished that some occasion might be offered . . . .

This represents the views of those statesmen and officials who were concerned with colonization as a remedy for existing defects in the government in Ireland. Both the Smiths accepted this view and did their best to make their plans and propaganda literature conform to it. Yet both were more concerned with the general problems of establishing a settlement in a distant and hostile land than with solving the problems of the English administration in Ireland, and it is this which makes their project of special interest as a forerunner of later experiments both in Ireland and America.

---

[32] Queen to Fitzwilliam, 24 Apr. 1572 (Carte MS 57, f. 475).

[33] The book "hath, as many like things do, passed forth without our knowledge or allowance either of us or of our privy council and therefore we have given order that the parties therein offending shall be punished for such a presumption," *ibid.*

[34] 3 Jan. 1572: Wm. Piers to Fitzwilliam (SP 63/35, 2); 8 Feb.: Wm. Piers to Fitzwilliam (SP 63/35, 23 (vi)); 27 Feb.: Fitzwilliam to Tho. Smith (Carte MS 57, f. 331); 6 Mar.: Sir Brian O'Neill to Fitzwilliam (SP 63/35, 32 (i)); 14 Mar.: Fitzwilliam to Burghley (SP 63/35, 32); 27 Mar.: Sir Brian O'Neill to Queen and to Privy Council (SP 63/35, 44–5); 27 June: Fitzwilliam and Ir. Privy Council to Queen (SP 63/36, 46).

[35] 10 Apr. 1572 (*Cal. S. P. For., 1583, & Add.*, 468–470; *Cal. Carew MSS, 1515–74*, pp. 419–420).

[36] 16 Apr. 1572 (*Cal. S. P. For., 1583, & Add.*, pp. 475–476).

[37] Indeed it appears probable that they were the first direct printed publicity in England for any business venture.

[38] Copy in Public Record Office of Northern Ireland.

In the *Letter*[39] overpopulation in England is put forward as a general reason for encouraging overseas expansion ("England was neuer that can be heard of, fuller of people than it is at this day"). We have here a fairly early example of a belief which was widely current in the latter part of Elizabeth's reign.[40] It is ascribed in part to the ending of monasticism and the consequent increase of marriages among the children of the landed classes. Other countries adjacent to England, such as France, Spain, and Scotland, are, it is argued, already adequately peopled or else are barren, so that English colonization there would only be possible if the populations were expelled. Ireland already belongs to the crown, is ripe for colonization and this task is "a sufficient worke for our age." In a tract intended to draw settlers to Ireland the Smiths naturally do not consider the possibilities of settlement in America.

In the supposed excess of population the most important elements, for the purpose of the authors of the *Letter*, are the younger sons of the nobility and gentry: "suche younger brothers," we learn, "as were wonte to be thruste into Abbayes, there to liue (an idle life), sith that is taken from them muste now seeke some other place to liue in," especially as primogeniture, "which giueth all to the elder brother," leaves them unprovided from their parents' estate. Now they find it specially hard to exist as there is a housing shortage, prices and standards of living ("excessive expence; both in diet and apparell") are rising, and it is almost impossible for them to "maintaine them selues in the emulation of this world with like countenance as the grounded riche can do."

Cheap and plentiful land was a primary attraction which was played up in the tract. Each subscriber would get at the least three hundred acres which would be a substantial farm in Essex.[41] With land at only a penny an acre rent, with some extra charge for maintaining soldiers, the scheme, it was urged, should be "a fit matche for younger brothers, such as haue but annuities, stipendes, and deade stockes to liue on." They could get a house and enough land, if they were resident on it, to give them a good living. "I cannot see," says the writer, "how Fathers that haue many sonnes, or landed men that haue many younger brothers, can do better . . . than to prefer them, and set them forthe in this jorney with me." Shortly after the publication of the tract, Sir Thomas Smith wrote to Sir Valentine Browne:[42]

> There was never a better nor more profitable and honourable a voyage for young gentlemen and younger brethern to make, Find them self one year, and take land to them and their heirs ten times more than they can buy in England on the price and as good.

He also told Fitzwilliam that he had seen great competition in the past for short-term leases of royal land in the Pale, but that "Now land can be had at once for ever at better cheap than the worst land in the English Pale."[43]

In the initial petition[44] the intention to make the colony another England in its social and economic structure was clearly expressed, and in the elaboration of the project this idea is constantly stressed. The city Elizabeth was to be a little London, first a centre for defence, then of civilization and trade. Round it would lie the parishes, each with one or a small group of substantial landowners in place of the squire, with its village church and parson, the craftsmen and labourers with their small holdings. To begin with, the landowners, though rich in corn and cattle from the first settlement, would not be able to make much money from their produce for a time. Later, a market could be worked up for corn in Ireland and possibly also in England, France, and Spain. The tenants and labourers would be largely but not wholly Irish. "It is thought best," Sir Thomas wrote to Fitzwilliam,[45] "the Englishmen to be chiefly sent armiger,[46] or else at the least citizens; but if some labourers be amongst them, to teach them the English manner of ploughing and saving of the hay, it will not be the worse." In the *Letter* gentlemen adventurers were told[47] "You may haue farmers out of the Ile of Man and othere poore men out of England, so they may be ayded at the firste with some stock of Corn and Cattel." At the end of 1572 Sir Thomas was promising to send over, early in the following year, not only soldiers but "husbandmen & plowmen to sow & plant the grownd,

[39] Hill, *op. cit.*, 409–410.
[40] *Cf. Proc. Royal Irish Academy*, **47**, C: 156–157, 1942.
[41] Sir Thomas Smith's home was in Essex at Theydon Mount.
[42] 15 Apr. 1572 (*Cal. S. P. For., 1583, & Add.*, 475).
[43] 21 Aug. 1572 (Carte MS 57, f. 42).
[44] Hist. MSS Comm., *De l'Isle & Dudley MSS*, II: 15.
[45] 18 May 1572 (*Cal. S. P. For., 1583, & Add.*, 489–490).
[46] I. e. of gentle birth.
[47] Hill, *op. cit.*, 410.

that ther might be some apparaunce of ciuilitie,"[48] and again "som Laborers"[49] were to be included in the 1574 expedition.

Sir Thomas Smith's personal adventure in 1572 was to be devoted to the exploitation of Irish timber with a view to its export to the continent. He told his son:[50]

> For the hundred pounds I have given for my adventure this year, I would you should take with you Thomas Smith, my godson, and one or two more of my brother George's sons if they will go . . . Those that go shall be horsemen. I will make it up the next year for one whole parish, that is 10 footmen and 5 horsemen, and would have it called Smith's Walden . . . I rather would have it either in Kilwarney or Kilult[51] where there is most store of great timber. And if you could have store of workmen, ye cannot be better occupied than to send to Bourdeaux or Nantes store of "clasbord" [clapboard] to make pipes and hogsheads.

"And as for the present necessitie and lack of many commodities of the Country which are in England euery where," the *Letter* said,[52] they were due to the backwardness of the Irish. Such conditions could be soon remedied:

> it may be replenished with building ciuill inhabitantes and traffigue with lawe, iustice and good order, what shal let that it be not also as pleasant and profitable as any parte of England, especially when it shall be furnished with a companie of Gentlemen and others that will liue frendly in felowship togither reioysing in the frute and commoditie of their former trauaile.[53]

The colony, indeed, was to be a true resettlement of English social life in Irish soil. It would have its own separate corporate existence and being, and the native inhabitants would fit smoothly into the social picture, humble and exploited but not too bitterly oppressed.

Great store was set to begin with on the Irish labourer as an asset to the colony: "the Churle of Ireland," said the *Letter*,[54] "is a very simple and toylesome man." The writer even thought that:

> the sweetnesse whiche the owners shall find in the Irish Churle giving excessively, wil hinder the countrie much in the peopling of it with the English Nation, makyng men negligent to prouide English Farmours.

Only the "wild" Irish were threatened by the colony, Sir Thomas Smith told Burghley—

> He that is contented with his own and will live quiet, and much more he that will labour for his living, shall be defended, cherished, yea, and enriched if he will.[55]

And again,

> The husbandmen, whom I understand they call there the churl, shall have his land to occupy upon such easy conditions as shall be thought meet, and not to be eaten out with coyne and livery or any such exactions, but contrary wise defended to the uttermost, that he may be as rich as he will.[56]

The early news of the Smith project so greatly alarmed the Irish and so irritated the Dublin administration that Sir Thomas was at pains to stress to Fitzwilliam the benevolent aim of the colony so far as the native population was concerned. He wrote:[57]

> It is neither sought to expel or destroy the Irish race, but to keep them in quiet, in order, in virtuous labour and in justice, and to teach them English laws and civility, and to leave robbing, stealing and killing one another, paying a rent to nourish the garrison and colonies. They should as farmers or copyholders have the use of the rest, without being eaten out with coyne and livery and bonaght or otherwise spoiled at the coming out of a rebel.

When, however, the Irish offered such stubborn resistance to the first settlers and when, finally, some of these very Irish "churls" employed in Thomas Smith's household turned on him and killed him, Sir Thomas Smith ceased to laud the peaceable qualities of the native population. While he did not turn to plans for their extirpa-

[48] Smith to Fitzwilliam, 31 Dec. 1572 (Carte MS 56, f. 42).

[49] Smith to Fitzwilliam, 21 June 1574 (Carte MS 56, f. 211).

[50] 20 May 1572 (*Cal. S. P. For., 1583, & Add.*, 490–492).

[51] Heavily wooded districts at the western edge of the territory and fringing Lough Neagh.

[52] Hill, *op. cit.*, 413.

[53] Compare Sir Thomas Smith to his son, 20 May 1572 (*Cal. S. P. For., 1583, & Add.*, 490–492): "This habitation together [in the city Elizabeth] engendereth civility, policy, acquaintance, consultation, and a firm and sure seat. Your tenants, farmers, churls and labourers of the ground may still go abroad and live as they can most for their commodity, and dispersed, yet I would they should at the first be by parishes, or rather two parishes together, where they shall dwell at the first appointment for more civility; for the manner of man is, the more they resort together, and have common profit or peril, the more civil and obedient they be; else they will be and grow beastly and savage, which hath been hitherto one cause of the ruin of Ireland."

[54] Hill, *op. cit.*, 410.

[55] 10 Apr. 1572 (*Cal. S. P. For., 1583, & Add.*, 468–470).

[56] 18 May 1572 (*Ibid.*, 489–490).

[57] 8 Nov. 1572 (Carte MS 57, f. 435).

tion he realized that the facile hopes of exploiting and reforming the Irish were too lightly grounded. By the time he was ready to dispatch a new expedition in 1574 his comments on the relations which should subsist between the colonists and the Irish were much more cautious. He told Fitzwilliam:[58]

> My chief order is, that they shall offer no iniury to eny Irish persone, nor take enything from them without payeng for it, but quietly build their howses, fortifie their towne, & plow their growndes, and be good neighbors, if the yrish will be so to them, Not to deny the yrish land from yere to yere of easie price & condicions/ Yf Iniury be voluntary offred, Then no reason it is but to defend & revendge.

The conception of the new English society overseas converting the Irish into good anglicised labourers had dwindled. The most Sir Thomas now hoped for was a dual society in which English and Irish would live and let live.

The success of the colony depended on the quality and number of the English settlers. Sir Thomas hoped in August 1572, even after his son's first contingent had melted to a mere hundred, that he would be able to have one thousand men well established and three thousand ploughs working by the time the patent ran out in 1579.[59] At the end of 1572 Sir Thomas was hoping to send his son the following summer "a better crue of Soldiars then yet he hath,"[60] although he had come to Ireland "weakely, late, & euill furnished this last yere."[61] The two hundred and fifty men despatched from England in March 1573 were described as "well armed weaponed vitailed."[62] Nevertheless good colonizing material was not easy to find and by April Sir Thomas was lamenting to Fitzwilliam that there were many people who were prepared to try to discourage good men from going: "Men," he said,[63] "be easier to be led from payne to ease, from labour to ydlenes, from adventuring to drinking and to lieng at home, then to travaile & seke abrode with danger & cost either honour or profite which they do not presently se." Fitzwilliam, who was sceptical about Thomas Smith's capacity to establish a colony, noted cynically in the margin of this letter, "The owld addage is true better to syt styll for nought then to labor for nought, I judge them wys which woll se how they do or waye beste the cost to profet, for a foll & hys mony is sone partyd."

Sir Thomas sent out the 1574 expedition with mistrust in his heart. The 1573 supply had never reached Ireland: his son had been killed and his colony scattered. He explained to Fitzwilliam that the divided responsibility given to his brother George and Jerome Brett was intended "to avoid strife & contention for the gouernement at the first," and he showed his doubts of Brett's reliability by saying "But if he should abuse hym self with insolencye (as I trust he will not altho mans nature is apt enough to it) it shalbe allwaies in my power to revoke that authoritie & to apoynt it to an other."[64]

As time went on Sir Thomas was more and more impressed by the disadvantages under which a private person undertaking a colony laboured. He had to place himself at the mercy of the adventurers and had little chance of redress if they played fast and loose with the expedition: "what can a subiect do who hath not power of commaundement, but must do all by consent & agreament?" he asked Fitzwilliam.[65] Then, too, he became impressed by the special difficulties and weaknesses of a colony in its infancy. Before the end of 1572 he was pleading with Fitzwilliam for his assistance in nurturing the settlement: "These weake & new planted thinges," he said, "do most require your cherishing."[66] Again in 1574 he asked the lord deputy to "be as a father to his pore colonye / which is a yong tree that hath bene oft cutt of when it began to grow / So I trust with experience & felyng of the precedent euills / will take suerer roote now at the last."[67] Despair was growing and a little later it burst out: "me thynks," he said, "by all wais and at all tymes these Yrish maters haue many hynderaunces and lets / Especially myne for the Ardes."[68] So many later promoters of colonial settlements both in Ireland and in America must have felt after long striving.

[58] 23 Mar. 1574 (Carte MS 56, f. 197).
[59] Smith to Fitzwilliam, 21 Aug. (Carte MS 57, f. 42).
[60] 31 Dec. 1572 (Carte MS 56, f. 42).
[61] 5 Jan. 1573 (Carte MS 56, f. 44).
[62] 13 Apr. 1573 (Carte MS 56, f. 49). The fleet of three ships, in fact, sailed towards Rochelle and evidently abandoned colonization for privateering.
[63] *Ibid.*
[64] 21 June 1574 (Carte MS 56, f. 211).
[65] 16 June 1574 (Carte MS 56, f. 197).
[66] Carte MS 56, f. 42.
[67] Carte MS 56, f. 211.
[68] 1 Aug. 1574 (Carte MS 56, f. 220).

VII

Finance was the rock on which most early colonizing ventures foundered. It was possible to raise for such ventures an initial capital which appeared adequate enough, but experience was to prove, time after time, that, in the first place, the greater part of the money would be frittered away in the delays and unexpected contingencies which arose before an expedition could be got to sea and, secondly, the continuous supplying and reinforcing of a colony until it could be self-supporting required a steady stream of capital over a long period which was unlikely to be forthcoming since there was little or no hope of a return to be speedily gained from it. The Smith venture illustrates, and for the first time in English experience, how a scheme for a corporately financed colony, which looked very well on paper, could be quite inadequate in practice. The terminable joint-stock trading ventures, developed during the previous twenty years, had had some measure of success owing to relatively quick returns on the working capital, providing an incentive, and the means, for its replenishment. It is not surprising that the joint-stock principle, since it worked well enough in the Muscovy and West Africa trades, should have been experimented with in mining and industrial projects. The Smiths were the first to attempt to apply it to colonization.

The initial petition envisaged the raising of a stock of between £12,000 and £13,000 "towardes the common charges of transportation, victualing, and fortification for the first yeare." Each man going as a horseman, or sending a fully equipped substitute was to contribute £20, and as and for a footman £12. The numbers anticipated were three hundred horsemen and five hundred to six hundred footmen.[69] In *The offer and order* and the *Letter* the financial scheme had been modified and elaborated. The basic rates of contributions were, for a horseman, £20 and, for a footman, £10, making, with an estimate of three hundred horse and four hundred foot, a target of £10,000. A new category of investor who would supply money only was introduced: for each £16 13*s* 4*d* thus subscribed the Smiths would equip and support a footman for a year. The subscriptions were to be entrusted to a treasurer and used as a common stock to provide shipping, food, and munitions of war as well as to pay the artificers ("Carpenters, Masons, Smithes, &c.") and hands ("as Cookes, Bakers, Surgeons, &c.") who would have to be employed. For lodgings under canvas until permanent buildings were erected horsemen would pay 20*s* and footmen 10*s*. All moneys not laid out in the first year were to be conserved and applied to the second year's expenses, but a second call of £10, £16 13*s* 4*d* or £20, as the case might be, could be made on the adventurers if the money was required for these. Investors were told that "Two yeeres charges is the vttermoste can passe without gaine" and they were promised the most economical administration possible.

To begin with, men came in rapidly. According to the Queen seven hundred to eight hundred men had been assembled at Liverpool by May.[70] That money was paid in much more slowly is evident from Thomas Smith's appeal to his father for cash at the end of April.[71] Adventurers turned up equipped to make the voyage, promising that their money contribution would be paid later and requiring to be fed and maintained for the time being from the common stock which, such as it was, was urgently needed for supplies for the expedition. When, on the eve of its departure, the fleet was countermanded by royal order the effect was disastrous. The great majority of the adventurers decided to cut their losses at once, refused to pay their subscriptions, and deserted to join the volunteer forces which Sir Humphrey Gilbert and others were raising to aid the Dutch. Those who remained loyal to the enterprise either hung on at Liverpool or dispersed for the time being to their homes. Thomas Smith went off penniless to London, leaving his equipment at Liverpool, to plead for permission to continue. There he was forced to borrow £150—"So yong gentlemen & vnwise be helped of marchaun*n*tes & vserers in London whiles all their land & living be gone in dettes and they shaken owt of all togither," said his father.[72] Finally, when Sir Thomas returned from France and was made Secretary of State, permission for the expedition to proceed was granted on July 16; but even then, as Sir Thomas grumbled later:

> I was fayne (after he had had a good round som of me before) to borow CC li. for him, and pay it aftirward, or els he cowld not haue gone to and owt

[69] Hist. MSS Comm., *De l'Isle & Dudley MSS*, II: 12–15.

[70] Queen to Fitzwilliam, 5 Aug. 1572 (Carte MS 57, f. 406); though Leicester says "at least 300" (Carte MS 57, f. 414).

[71] *Cal. S. P. For., 1583, & Add.*, 484–485, 487.

[72] 12 Apr. 1573 (Carte MS 56, f. 49).

of Lirepole, Where those his sowldiers had lyen so long attending his coming from the cowrte, and spent him so miche that I think the CC li. could scarsely lose him from thence.[73]

Apart from the £100 which Sir Thomas advanced in May[74] and the £350 borrowed in London we hear of a few odd subscriptions to the enterprise. Lord Burghley backed it with the considerable sum of £333 6*s* 8*d* as an adventure for twenty ploughlands in the Ards.[75] This represented the payment for twenty footmen to be supplied and equipped by the Smiths for a year. Sir John Thynne of Longleat, an old friend of Sir Thomas, was also an investor. Thomas Smith wrote to him on July 19 that he had just received his despatch from Court and was leaving for Liverpool three days later to embark; he says:

> There I look for your two horsmen to meet me as ye promised at your owne howse therin. If they be with me at Lyverpoole the last of this moneth it shall be well and soone enough/ This I pray you do / At the least that the men be there furnished / And if they cannot bring the money [i. e. the £40 of his adventure] which willingly as very needfull I wold faine have also Let them bring with them a bill of your hand for the same to be payd at London as sone as conveniently ye can.[76]

Leaving Liverpool at length with little more than a hundred men at the end of August[77] Thomas Smith and his little company had no ready cash left for purchases in Ireland, and one of Smith's earliest acts there was to borrow £100 from Lady Fitzwilliam, wife of the lord deputy, together with some wheat from Fitzwilliam,[78] for the repayment of which Sir Thomas would accept no responsibility. In October the latter said that he expected Thomas Smith's partners to pay in their outstanding subscriptions to his London representative, but nothing had been heard of the money: he himself denied indignantly that he had ever acted as his son's treasurer or receiver or had handled any of the adventurers' money.[79] By April 1573 Sir Thomas was expressing his disgust at the "evill husbandry" and lack of foresight shown in the administration of the adventurers' finances[80]—so much for the cheap and efficient handling of the capital promised when the common stock was opened at the end of 1571.

Nevertheless, Sir Thomas was not quite so disinterested in the financial concerns of the colony as he tried to make out to Fitzwilliam. Early in 1573 he made a big effort to raise a new supply of money and men for his son. More adventurers were enlisted and a certain amount of money was collected to fit them out. Again there were delays owing to the promised money not being forthcoming and though the expedition left the Isle of Wight on March 23, it never reached Ireland.[81] Sir Thomas Smith's final effort to mobilize support for the venture was made between March and August 1574. Once again a considerable sum must have been raised in order to despatch one hundred and fifty men across the Irish sea, but no details are available beyond the fact that many of the adventurers once again failed to honor their obligations: "this yere," Sir Thomas complained to Fitzwilliam, "I haue not half the p*ro*mises and bands made betwixt me and myne adventurers kept."[82]

The scheme of financing a colonial venture by means of a common stock raised by private adventurers, which had sounded so promising in the prospectus and in the early months after its opening, proved inadequate and unsatisfactory, but the Smiths' pioneering difficulties and failures did not deter later adventurers, both in Ireland and America, from making similar, and equally unsatisfactory, experiments.[83]

---

[73] *Ibid.* To which we must add some £80 needed to release a ship of Thomas Smith's, driven into Beaumaris in the winter and provided by his father.

[74] *Cal. S. P. For., 1583, & Add.*, 484–485, 487.

[75] Hist. MSS Comm., *Cecil MSS*, XIV: 73; undated but probably 1572.

[76] *Wiltshire Arch. & Nat. Hist. Mag.* **18**: 262, 1879.

[77] Carte MS 56, f. 49.

[78] Carte MSS 57, f. 612; 56, f. 49.

[79] Carte MS 56, f. 49.

[80] *Ibid.*

[81] Sir Thomas Smith to Fitzwilliam, 12 Apr. 1573 (Carte MS 56, f. 49) and a tantalizingly incomplete account in Strype, *Sir Thomas Smith*, 135–136.

[82] 16 June 1574 (Carte MS 56, f. 197).

[83] It may be asked what profits the Smiths themselves hoped to make from the successful prosecution of the enterprise. Most would arise from the difference between the rent to be paid by the adventurers to the Smiths and what they were to pay to the crown. Adventurers were to pay 1*d* sterling per English acre of arable land (i. e., 4,840 square yards); while the Smiths were to pay the Queen 2*d* Irish (1½*d* English) for each Irish acre of 10,240 square yards. In addition all non-arable land, containing valuable timber, was at the disposition of the Smiths without payment of rent to the crown, though Thomas Smith was prepared to include the non-arable land in the adventurers' grants (*vide* Sir Thomas' replies to his son's articles, 18 May 1572, SP 70/146, 109: "I take yow write that he shall have wood medow & pasture, payeng nothyng to us. I wold they had it in the Ard then, not in Kil-

VIII

The framework and organization of the colony were planned on a pattern not dissimilar to many later American ventures. Sir Thomas Smith and his son were to be feudal tenants-in-chief of the crown, owing rent and military service, but having considerable local rights of jurisdiction. The adventurers, holding lands from them, were to be their feudal subtenants. Sir Thomas, with his son as his effective deputy, was to be "Colonel," keeping the military leadership and executive and judicial powers in his own hands. The grantees were to appoint the treasurer who was to handle the common stock in which the investments of the adventurers were to be pooled. But the organization was not to be wholly authoritarian: from the beginning it was conceded that the adventurers should have some part in drawing up the agreed code of procedure and discipline which was to be enforced,[84] while the lands were to be distributed by lot.[85]

It is evident, however, that as soon as adventurers came forward they began to demand some more positive share in the administration of the venture. As early as 10 April 1572 Sir Thomas was writing to his son:[86]

> Touching those who require unreasonable things, you have made a good determination, methinks, and I would not have you swerve from it, lest others, who are contented with reason, should be offended, while he who demands more than reason will not be contented, and will ever ask more and more, therefore let them go, as men unreasonable and unruly.

And six days later he added:[87]

> To them that require things unreasonable, and would take from us that which the Queen hath given, and set themself either above or equal with us, you may answer plainly you cannot do it, for it is mine interest as well as your, and you cannot give mine interest away, nor give no other wise to no man than is comprised in the indentures betwixt the Queen's Majesty and us; for they must needs hold of us as we hold of her Majesty. If they will be colonels, let them sue out a patent of some other place as we have done this.

The quarrel thus referred to was partly concerned with the military command of the expedition which Sir Thomas was determined should remain in his son's hand, but, at the same time, he was not averse in principle to his son sharing part of the responsibility for the administration of the venture with the adventurers, saying:

> Of taking of counsellors to you, I cannot mislike it, and to communicate to them and take their advice, especially when you be settled and have begun your fort *Elizabeth*, . . . for you must not be without a certain senate in peace-time.[88] In war not so. The captain's designs and stratagems must not be known to many, for the most part but to himself only.

Shortly afterwards Thomas Smith wrote to his father advocating a scheme whereby thirty of the principal adventurers should be selected as his assistants in the enterprise. Sir Thomas replied[89] "That which you like so well of the 30

warney nor Kilult"). Thirdly, there would be profits from the land which they selected as their own adventure, and finally, incidentals like profits of justice and letting of fisheries.

[84] "And to take al occasion of Quarels, Mutineries, or other disorder, . . . he hath promised to cause one book of orders or Discipline to be drawen, by the aduise of the best Captaines and shall be reade vnto the whole companie, Whiche after it is allowed and agreed to by them, shalbe kept safely as the Statutes of this iorney, and according to the letter of that Booke, shall all misdemeanours of the Campe be punished" (Hill, 414). It appears that Sir Thomas drew up a complete draft of the regulations for the expedition and the government of the colony, but it has not proved possible to locate it (Strype, *Smith*, 133–134).

[85] Hill, *op. cit.*, 414.

[86] *Cal. S. P. For., 1583, & Add.*, 467–468.

[87] *Ibid.*, 476.

[88] Compare Sir Thomas' views on the English Parliament (*De republica Anglorum*, ed. Alston, 48).

[89] *Cal. S. P. For., 1583, & Add.*, 490–492. Thomas' 17 queries sent to his father have not survived and the calendar does not give his father's replies in full. The latter (SP 70/146, 109, for which I am indebted to Mr. C. S. Drew of the Public Record Office for a transcript) are not fully self-explanatory, but throw light on the points at issue. The first two read:

To the first

> Do yow meane as assistaunts to the Colonells ther heyres & successors & so that they & ther heires beyng of lawfull age shalbe assistaunts, that is senators aldermen or cownselers to the Colonells & ther heires? Yf yow do so, it were better they were c. then xxx., becawse som may be away, som sick, to yong or mad, or have other impedyments. Your meanyng is, as I take it, that those should be ever after as *patricii* or *senatores* or lords of thassemble [below, in answer to the 17th query, he gives *assistentes coloniae* as an alternative title]. Or els I can not tell what yow do meane.

To the second

> Whie should yow limit the tyme & power for one yere & not duryng the hole vij. yeres, what tyme yow have limitted to yow of spredyng your colonye? For my part I dowte not but from yere to yere, upon such condicions yf I may live & tary in England, yow shall have every yere more then other that will com to yow; & towchyng the dispendyng of vj^{c}. markes by yere, yf yow meane in

assistants, I cannot so soon allow, nor do I utterly disallow it . . . , but it may be suspended until I come home." At the same time Sir Thomas was sufficiently favorable to the idea to sketch out the special responsibilities of the assistants in the city Elizabeth:

> . . . where it is meet that each assistant have a place of ground to make his palace or chief residence, of our giving; . . . and then he to hold likewise his land and tenure of assistance, aid or patriciate of us and our heirs, by such tenure as is afore, with condition to maintain in the chief castle or citadel of the city Elizabeth, one tower against all the Queen's Majesty's enemies.

We know very little further of the matter, except that it was proceeded with after Sir Thomas Smith had returned to England and we find Thomas Smith writing to Sir John Thynne on July 19[90] "I committe the rest of our matter for the assistauntshippe to my father."

The organization of the enterprise had now a certain amount in common with that of the overseas trading concerns, like the Muscovy Company. Sir Thomas and his son stood in the place of the governor. The assistants, with the governor, his deputy, the treasurer, and other officials, would form the executive and administrative authority, responsible for the expenditure of the common fund and the making of rules for the conduct of the colony. But there is no mention of any general court of all the adventurers. Sir Thomas evidently preferred an oligarchical structure to one in which the rank and file of investors would have any say. From what we know we may assume that the assistants were not elected in any way but were merely chosen by Sir Thomas and his son from among those adventurers who had made the biggest contributions. Sir Thomas Smith's ideas of how an administration should be developed in the colony are not unlike those which Sir Humphrey Gilbert drew up for his American colony in 1582,[91] although he envisaged some element of democratic choice in the selection of councillors and officials.

As in many other respects practice, as regards administration and organization, differed considerably from theory. The treasurer appointed by Thomas Smith apparently ceased to function after the expedition sailed for the Ards. How many of the assistants accompanied him we do not know, nor are we informed how they functioned in Ireland or whether those left behind in England played any part in directing the enterprise. There was some dissension among the little band of adventurers in the Ards,[92] but we do not know in what respects this reflects a division in the executive. Until his death Thomas Smith did wield some measure of authority over his followers, the legal basis for which was the commissions granted to his father and him by the Dublin administration. A commission to them as "colonel" empowered them to lead soldiers and colonists into the Ards, to govern the soldiers and inhabitants, to determine all civil cases except pleas of land, and to punish all criminals except traitors and coiners. Another commission enabled them to exercise martial law.[93] In England, so far as we know, Sir Thomas acted as the sole executive, although, on the pretext that there was still supposed to be a treasurer in charge of the common stock of the expedition he refused to pay his son's debts. There is no evidence to enable us to determine whether any of the four captains of the adventurers assembled to reinforce the first colony early in 1573 was given a special status in the administration of the enterprise, but in any case they never reached Ireland. In the Ards Thomas Smith's most intimate and important associates were his uncle, George Smith, citizen and draper of London, and his three sons. After Thomas Smith has been killed, Denys Smith, one of his cousins took command of the surviving colonists, while George Smith and his remaining sons returned to England.[94]

England I do not se what it is to the purpose, & I dowte so whether Mr. Carleton may be one & som of thothers named. But if yow meane so mych in the new colonye in Ireland, that wilbe very miche mine opinion, if yow meane as it is paid to the Quene. The rediest & best way is for yow & your enterprise that who so ever by hym & his folowers will take upon hym to possesse x. parishes, which is to bryng cx. fotemen & l. horsmen, should be one of the assistaunts & enjoye such privileges as yow speak of & then he shall have one hondreth of his owne his cowrt & the quenes leate &c., as is in your instructions. They that bryng under, I se no reason why they should clayme so myche privilege: all this charge is but ij^{m}. li. But if yow will bryng it to v. parishes, then yow must alter your instructions, which I can not so well like.

[90] *Wiltshire Arch. & Nat. Hist. Mag.*, **18**: 262, 1879.

[91] *Cf.* Quinn, *op. cit.*, 59.

[92] SP 63/40, 8, 37, 75–6; 41, 61.

[93] Both commissions are dated 29 Sept. 1572 (*12th Rep. Dep. Keeper of Rec., Ire.*, fiants 2149–2150).

[94] Essex to Burghley, 20 Oct. 1572 (W. B. Devereux, *Lives and letters of the Devereux, Earls of Essex*, I, 40–42, 1853); Essex to Privy Council, 28 Oct. (SP 63/42, 58). George Smith's occupation is mentioned in *Cal. S. P. Domestic, Add. 1566–1579*, 531.

When, in 1574, Sir Thomas Smith made his final attempt to establish a colony in the Ards he did not try to revive the elaborate system of administration envisaged in 1572, but concluded that something much simpler would be adequate for his purpose. Such common funds as were collected were evidently applied solely to the costs of transportation: thereafter each captain, acting as a principal adventurer and in charge of a group of colonists, was, himself, to be responsible for their feeding and maintenance.[95] The most important adventurer, Captain Jerome Brett,[96] was to bring with him sixty footmen, amounting to nearly half the total force, "at his owne charge & fyendyng, to inhabite the contrey."[97] The government of the colony was to be committed to Brett and George Smith. The latter was to be the representative of Sir Thomas Smith in all matters relating to the organization of the colony and the distribution of lands. To Fitzwilliam he said of him:

> In steade of my sonne I haue sent now my brother George *with* his iij sonnes / In him I put my most confidence for governement & keping of my deseignes, for he is of good age, & past the folies of youth, quiet of nature, and like to be therein myne heire, and that to be his porcion if god send him & me good fortune. . . . Altho my brother be not Colonell by patent, Yet he may by my consent give away my land given to me & myne heire, to others & their heirs, vpon suche condicions as are limited.[98]

Brett was to be the military commander, but was to have no authority in other matters without George Smith's advice and consent:

> Hierome Brett for Martiall affaires of the Colony, as being brought vp in Ireland, I am fayne to put in the next trust. . . . I trust now being of good yeres, long experience, & well beaten *with* the troubles of this world, he will with wisdome & good order recover all *which* hath bene stayned & lost, and get both praise & *profite* to him self. . . . In matter of the Colonye & the quiet governement I haue ioigned my brother George *with* hym, for the assignyng & allottyng of the land to eche *per*sone / that as in maters of warre / I trust hym alone for his skill / in other matters he shall haue no authoritie but *with* my brothers advice & consent who is like to have most interest in it if it be well done.[99]

The grant of exclusive authority to George Smith and Brett was qualified by the hope that they would take advice if they were in difficulties. Sir Thomas said of Brett "I dowte not but he will vse the advise of the wiser sort of the Colony & do nothing *with*out it,"[100] while he also hoped that advice from Captain William Piers, former constable of Carrickfergus, and Francis Lany, victualler to Essex's army in Ulster, who were expected to join the colonists, would be given and taken.[101] Sir Thomas' doubts about Brett's capacity are evident from the above quotations, and when he asked Fitzwilliam for a renewed commission as colonel and for a commission of martial law he wished them to be in his own name, with Brett mentioned as his deputy,[102] but Fitzwilliam decided there were legal difficulties in the way of this and on July 24 Brett received a commission of martial law alone for himself.[103]

Little is known of the organization of the colony in the months after its arrival in the Ards in August 1574. Brett soon quarrelled with George Smith and succeeded in driving him out of the colony until he, himself, was forced to leave Comber and take refuge in the Lower Ards. From his letters Brett appears to have been an incompetent braggart. Finally, in April 1575, Sir Thomas wrote to Fitzwilliam denouncing Brett for trying to ruin the colony and asking that all authority under the commission of martial law be revoked from him. Brett was merely to be left to hold such lands as he had contracted for in his adventure. In his stead Sir Thomas hoped that the Earl of Essex would be willing to take on responsibility for the government of the colony, and indeed Essex agreed in principle to do so on April 26.[104] But Essex had had more than enough of the north of Ireland since his arrival there in 1573 and paid no attention to the Ards. The colony and its government died a natural death, though Sir Thomas transmitted his rights and titles to his Irish lands to his nephew, William, whose

[95] "Eche of my Coloners to *pro*vide for him self, at the least eche Captain for him & his & to kepe no more then he shalbe able at all tymes of his owne to feede" (Smith to Fitzwilliam, 16 June 1574. Carte MS 56, f. 197).

[96] Brett had for some years been putting forward projects for the colonization and reformation of Ireland (SP 63/26, 52–3; 27, 21; 28, 21; 40, 20–22, 55–57).

[97] 21 June 1574 (Carte MS 56, f. 211).

[98] Carte MS 56, ff. 197, 218.

[99] Carte MS 56, ff. 197, 211.

[100] Carte MS 56, f. 211.

[101] Carte MS 56, f. 197: for Lany see *Cal. Carew MSS, 1515–74*, I, 487–490.

[102] Carte MS 56, ff. 198, 211, 218.

[103] *12th Rep. Dep. Keeper Rec., Ire.*, fiant 2437.

[104] 11 Apr. 1575, with notes by Fitzwilliam (Carte MS 55, f. 133).

father may have died before Sir Thomas, and whose last attempt to establish a settlement ended in fiasco in 1580.

IX

Like most of the early colonizing projects the Smith venture is of interest for its promise rather than its performance. The special conditions in Ireland where there was already an English administration, with some authority in the region it was intended to colonize, complicated and, in this instance, helped to stultify the activities of the promoters and adventurers. In any event, the organization and financing of the scheme were amateurish, defective, and incompetent in the extreme. The special interest of the episode lies in the fact that Sir Thomas Smith's ideas on colonial policy were not particularly directed towards the solution of peculiarly Irish problems, but to those common to colonial enterprise in general, and might have applied equally to a colony in America. It is the conscious imperialism which lay behind the specific plans of Sir Thomas Smith and his son which is significant, and it is remarkable to what an extent they anticipate the Hakluyts, Sir Humphrey Gilbert, Sir Richard Grenville, and Sir Walter Ralegh in their approach both to the general and the particular problems of colonization. They were not entirely original in that approach since so much discussion of Irish colonization had taken place before 1571, but they did crystallize and state for the first time in a general form many of the arguments which later became the stock-in-trade of colonial promoters. Unsuccessful as he was in the practical application of his schemes Sir Thomas Smith's ideas on colonial policy add another facet of interest to the many-sided life of Queen Elizabeth's learned Secretary of State.

REMOVING SOME OF THE BARRIERS TO CROSSABILITY IN PLANTS[1]

ALBERT F. BLAKESLEE

Smith College Genetics Experiment Station, Northampton, Mass.

(*Read in abbreviated form, November 18, 1944*)

For some years the writer and his associates have been interested in the evolution of species within the genus Datura, a group of plants which includes the common Jimson Weed, *Datura stramonium*. Since the hereditary units which distinguish species one from the other are located in the chromosomes, we have felt that the evolution of species could best be understood by a study of the evolution of their chromosomes. A method of determining evolutionary changes which have occurred in chromosomes is to compare them in hybrids with a standard species which in our group has been *Datura stramonium*. Unfortunately, this standard species will not hybridize with many other species of Datura. In fact, species hybrids within the genus are relatively difficult to secure. Sometimes we have obtained only a single viable hybrid seed after many hundred separate pollinations. Why hybrids sometimes can be secured, though rarely, is a natural question which we have not yet been able to answer.

It is sometimes profitable to restate a problem from a new angle and we now are asking what are the factors which prevent hybridization, with the hope that it may be possible to overcome some of the various barriers to crossability. These will be discussed in the following sections.

1. GEOGRAPHICAL SEPARATION

Species which do not grow near together cannot be expected to hybridize in nature. The obvious way of overcoming this barrier is to bring the two species into cultivation in the same place and to make the desired pollinations. Thus we have secured seed from a species of our group, *D. leichhardtii*, which is known to grow wild only in Australia where no other Daturas are native, and grew it in our garden and greenhouse. We succeeded in getting it to take part in the formation of more species hybrids than any other Datura.

2. NON-FLOWERING DUE TO LENGTH OF DAY

The attempt to secure propinquity and therefore the opportunity for hybridization with another species by moving one of the prospective parents does not always work. The moved species may fail to flower. Thus, certain species in temperate regions such as the common garden radish will not flower in the tropics, while certain tropical species will not flower in gardens in our latitude before they are checked by frost. This behavior was explained in 1920 by Garner and Allard who discovered that there are long-day plants which need a long daily illumination for flowering, and short-day plants which will flower only when the days are short. Fortunately, long-day plants, such as Portulaca and the Yellow Daisy, can be made to flower in the short days of winter in greenhouses in our latitude, or in the summer tropics, by lengthening the day by means of artificial light. Short-day plants may be brought to flower during long days by decreasing the length of day through the use of dark rooms. By adjusting the length of day it is possible to get a long- and a short-day species to flower at the same time and thus to overcome the barrier to crossability imposed by the different length of day requirements. All the species of Datura, except *D. meteloides*, which is a long-day plant, are uninfluenced in flowering by the length of day.

3. SPECIES FLOWER AT DIFFERENT TIMES

Unless two species flower at the same time they cannot be expected to hybridize in nature. This barrier may be overcome in a number of ways. (*a*) The later flowering species may be forced to flower earlier. Chilling of Iris, for example, is used commercially to induce early flowering. Lilacs have been brought to bloom months before the usual time by treatment with ether. Flowers of Forsythia may be secured in winter or early spring by merely bringing into a heated house cut

[1] Contributions from the Department of Botany, Smith College, New Series No. 17. This investigation was supported in part by the Carnegie Institution of Washington and by a grant from the Penrose Fund of the American Philosophical Society.

twigs which contain flower buds. The writer in attempting crosses with conifers has accelerated the shedding of pollen of late flowering species by bringing twigs into a heated greenhouse and has held back the pollen of early species by keeping twigs in a refrigerating room. (*b*) Adjustment of length of day already discussed above has been used to ensure simultaneous flowering of two species which normally flower at different times. (*c*) Pollen storage under proper conditions may enable crosses to be made between plants the flowering periods of which are widely separated. There is considerable difference in the length of time during which pollen remains alive and functioning. In corn the pollen usually dies within a day from the time it is shed and no method apparently has so far been devised to prolong greatly its viability. Pollen of some species normally remains alive for considerable periods. Thus, the writer has kept pollen of Jack Pine (*Pinus banksiana*) in the laboratory for over six months without loss of its power of germination. By proper methods of storage the life of the pollen of many species may be greatly prolonged. By special treatment it is possible with grapes and apples to use the pollen of late varieties in crosses with early varieties the next year (9).[2] Pollen of *Datura stramonium* keeps viable for about 10 or 11 days under laboratory conditions. By storing the pollen at a temperature of 7° C. and a relative humidity of 30 per cent it was possible to keep the pollen capable of taking part in fertilization for 120 days. A lower humidity (0.005 per cent) and a higher humidity (60 per cent) at the same temperature caused the pollen to lose its viability sooner.

4. VARIETAL DIFFERENCES MAY PREVENT HYBRIDIZATION

We have several races of *D. leichhardtii* secured from seeds collected in Australia. The first race when used as a female parent crosses readily with *Datura discolor*. The second race of *D. leichhardtii* fails to give viable seeds when pollinated by *D. discolor*. The two races are very similar and individual plants cannot be distinguished as to race by outward appearance. Our experience shows that if the second race of *leichhardtii* had been the one with which we had first attempted to secure a cross with *D. discolor*, it would have been wise for us to have tried other races of this Australian species with the hope of making a successful cross with a race of such a constitution as Race I showed itself to be. We have overcome the poor crossability of *leichhardtii* II in another way. *Leichhardtii* II had a pair of modified chromosomes which we wished to compare with chromosomes in hybrids with other species. We accordingly back-crossed *leichhardtii* II several times to *leichhardtii* I, so that ultimately we secured a race of *leichhardtii* which had the modified chromosomes of the second race and the characteristics of *leichhardtii* I which favor crossability.

5. SELF AND CLASS INCOMPATIBILITY

Not only may plants be prevented from crossing on account of being too distantly related, but also on account of being too closely related. Thus, many plants are self-sterile and will not set seed when pollinated with their own pollen. This is true in our experience with the Yellow Daisy (*Rudbeckia hirta*). Furthermore, the offspring of a cross between two self-sterile plants may show incompatibility classes such that two plants in the same class will not be able to cross with each other. Self and class incompatibilities may be factors of considerable importance in a breeding program. Thus, if a single plant of the Yellow Daisy were brought into a region where there were no other plants of this species, no offspring could be obtained. If two plants of this species were brought together without the opportunity of crossing with others of the same species they might still fail to set seed if they happened to be related and belonged to the same incompatibility class. Inbreeding in the Yellow Daisy not only develops incompatibility classes, the members of which cannot cross, but also greatly weakens the vigor of growth of the individual plants. The weakness due to inbreeding and the establishment of incompatible classes may be overcome by collecting seeds from a relatively large number of individual open-pollinated plants which are selected for vigor of growth.

6. SEPARATION OF SEXES

Most plants are "hermaphroditic," that is, they have both male and female organs (stamens and pistils) in the same flower. A few are "dioecious" and have the sexes separate. Thus, the Box Elder (*Acer negundo*) is either a male with only staminate flowers or a female with only pistillate flowers. We have never seen sex inter-

[2] The numbers in parentheses refer to the corresponding items in the References.

grades in this species which bore both male and female flowers. An isolated Box Elder, therefore, whether male or female, could not be expected to set seed since it would have none of its own species near by with which it could cross. The isolation of such female trees might facilitate hybridization with other compatible species. All the Lombardy Poplars in this country are male trees and hence never set seed. They have been propagated vegetatively from a mutation of the European Black Poplar which happened to be a male. In many dioecious species, separation of the sexes is not so complete and it is often possible to find some male flowers on predominately female mulberries and willows, for example, as well as occasional female flowers on male individuals of such species. Schaffner (15) by altering the length of day was able to reverse the sexes of hemp both toward male and toward female. The common Campion (*Melandrium dioeca*) is dioecious. The female has two X sex chromosomes; the male has an X and a Y sex chromosome. By the use of colchicine, Warmke and the writer (17) were able to double the chromosome number of this species and by proper breeding procedure to secure a plant with 4 X's and a single Y. It had occasional male flowers but most were hermaphroditic flowers which were selfed and gave rise to

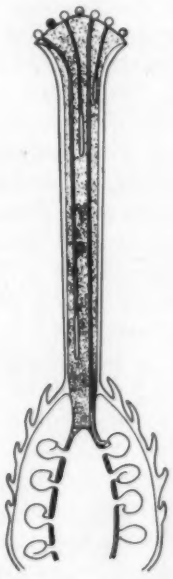


FIG. 1. Diagram of pistil with terminal stigma, connecting style and basal ovary. Pollen tubes from the germinated pollen grains on the stigma grow down through the style. One tube is shown to have entered the ovary and approached an ovule into which it is in position to discharge its sperm cells.

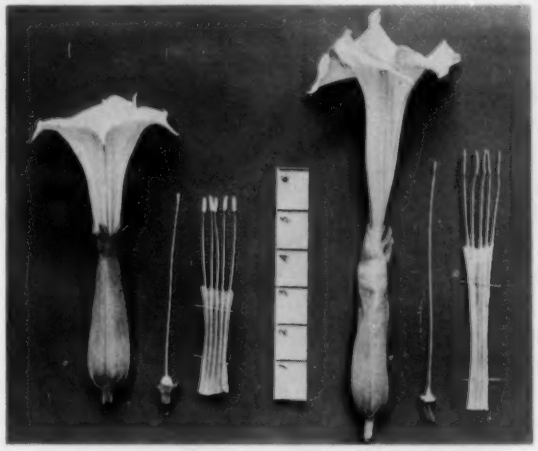


FIG. 2. Intact flowers with isolated pistils and stamens. Left, *D. inoxia;* right, hybrid, *D. inoxia* × *Brugmansia suaveolens*. Scale is marked in inches.

other similar plants in the next generation. By changes in the number of the sex chromosomes it was thus possible to overcome the barrier to crossability interposed by the separation of sexes.

Before discussing further barriers to crossability it will be desirable to consider for a moment some of the problems the plant must solve before fertilization is possible. When the flower is ripe, the anther sacs of the stamens open and shed the pollen. At the same time the pistil is usually mature. Figure 1 is a diagram of a Datura pistil showing pollen grains, pollen tubes, and ovules. Pollen grains germinate on the stigma which is the receptive tip of the pistil, producing long tubes which grow down inside the slender style and after entering the ovary burst and let out sperm cells which unite with the egg cells within the ovules. The result of this sexual fusion is the first cell of the embryo. The ovule with the embryo becomes the mature seed.

The dissected flowers in figure 2 show the length of style through which in some species the pollen tubes must grow as a prerequisite to fertilization. In the genus *Datura* the pistils range in length from about 30 mm. (1¼ inches) for *D. leichhardtii* to about 190 mm. (7½ inches) for *D. meteloides*.

7. POLLEN FAILS TO GERMINATE

A critical stage leading to fertilization is germination of pollen. Crossing between species is commonly blocked by failure of pollen of one species to germinate on the stigma of another species. In a race of *D. stramonium* in which the

pollen grains were glued together in a brittle mass and were incapable of germination on the stigma, we overcame the difficulty by the simple expedient of fastening the pollen masses to the stigma with flour paste. Since pollen can be readily induced to germinate in artificial media, it should be possible rather easily to overcome the barrier of non-germination of pollen on a foreign stigma.

8. POLLEN TUBES BURST

Bursting of pollen tubes within the style is a common phenomenon. When pollen from a normal 2n parent is applied to the stigma of a tetraploid (4n) Datura, capsules and seeds are formed. We are dealing here with the compatible cross 4n × 2n. If we make the reciprocal pollination and apply pollen from a tetraploid (4n) parent to a normal 2n stigma, it is practically certain we shall secure no seeds. Buchholz (5) has shown that the reason why 2n × 4n is an incompatible cross is that the pollen tubes derived from the 4n male parent burst in the 2n styles and are put out of commission before reaching the ovary. The bursting of the pollen tubes in this cross has been overcome and 2n × 4n changed from an incompatible to a compatible combination by the work of Satina on periclinal chimeras (14, 1). Periclinal chimeras are unusual forms of plants in which the cells of the outer skin, for example, may be entirely different in nature from those of the inner layers, in fact may belong to different species as is the case in "graft hybrids." Periclinal chimeras have been induced in Datura by treatment with colchicine. Some have the number of chromosomes doubled in the first or epidermal layer and not in the other two germ layers. The first layer, Dr. Satina has found, forms the transmitting tissue within the style through which the pollen tubes grow. Hence, the style of a 4n, 2n, 2n periclinal chimera (the chromosomal numbers of the 3 layers are indicated from outside in) should act like a pure 4n female parent so far as its reaction to pollen tubes from a 4n male parent is concerned. As a matter of fact, pollen tubes from a 4n male grow readily without bursting in styles of a periclinal chimera of the type mentioned which has a 4n epidermis and take part in fertilizing the egg cells which are derived from the normal 2n germ layer. This example of overcoming the barrier to crossability has to do with crosses between chromosomal types in a single species, *Datura stramonium*. Doubling chromosomal number of the female parent has prevented bursting of pollen tubes in styles of a different species. Thus, one of our graduate students, Miss Carmen Sanz, has found that, during an 18-hour test, most of the pollen tubes of the tomato burst in normal (2n) styles of *D. stramonium*, but that most of the tubes grow without bursting in the styles of a 4n *D. stramonium* during the same period (12).

9. POLLEN TUBES GROW TOO SLOWLY TO REACH OVARY

Buchholz (7) has shown that the species of Datura differ not only in lengths of pistils but also in speed of pollen-tube growth within their own styles. Thus, the pollen tubes of *D. inoxia* which has a pistil length of 150 mm. have a growth rate of 3.3 mm. per hour at 19° C., whereas pollen tubes of *D. quercifolia* which has a pistil length of 40 mm. have a growth rate under similar conditions of only 1.9 mm. The species with the longer style has faster growing pollen tubes. Pollen tubes with a slow growth rate are at a disadvantage in growing down a long style of another species, not only on account of the distance involved but also because of the fact that pollen tubes generally grow less rapidly in styles of another species than in those of their own. Slow-growing pollen tubes may be eliminated by the styles dropping off before the tubes reach the ovary. Miss Sanz has made tests of pollen-tube growth of a considerable number of species in pistils of *D. stramonium* after 18 hours at 26° C (12). She groups the pollen behavior into four main types: (*a*) pollen fails to germinate (2 species of the family *Solanaceae* to which Datura belongs, 35 species of 20 other families); (*b*) pollen germinates but all tubes burst in style (3 species of *Solanaceae*, 2 species of 2 other families); (*c*) about half the pollen tubes burst but the rest grow (5 species of *Solanaceae*, 4 of 3 other families); (*d*) most pollen tubes grow without bursting during the 18 hour-test (4 species of *Solanaceae*, 8 of 5 other families). The growth of the pollen tubes which failed to burst was generally too slow to reach the ovary for many days but the tubes of a few other genera grew half as fast as those of *D. stramonium* in its own style. It is possible that the barrier of slow pollen-tube growth may be overcome by the method of shortening and splicing styles worked out by Buchholz (6).

10. POLLEN TUBES REACH OVARY BUT FERTILIZATION FAILS TO OCCUR

This barrier has not yet been determined in Datura but its possible occurrence is being investigated in certain incompatible crosses.

11. FERTILIZATION OCCURS BUT DEVELOPMENT ARRESTED AFTER FEW CELLS

When a 4n Datura is pollinated with pollen from a 2n parent, practically all the egg cells are fertilized, but only about 1 per cent develops into viable seeds. Most abort after formation at most of 4 to 8 cells (11). Why so high a proportion are unable to develop further and why the favored few are able to develop into normal seeds which produce 3n offspring are as yet unknown.

A more extreme case is the attempted cross *D. stramonium* × *D. metel*. Hundreds of attemps have never yielded a viable seed though an occasional small seed-like body has been produced. Satina (13) has found that most of the egg cells are fertilized and embryonic growth is started, but the embryos generally abort before the 8-cell stage. Here, again, we are as yet ignorant of the causes of the early abortion. There are doubtless other crosses, at least in Datura, in which abortion occurs after fertilization and the formation of only a few cells. The determination of fertilization and early embryonic condition necessitates sectioning and detailed study which has been made for few incompatible crosses.

12. EMBRYO DEVELOPMENT CONSIDERABLE BUT GROWTH ARRESTED BEFORE FORMATION OF VIABLE SEED

As pointed out in an earlier paper before the American Philosophical Society (4) this barrier can be overcome in many cases by dissecting out the arrested embryos and cultivating them on artificial media. Embryo culture is becoming of increasing interest to plant workers (2) and our group is using it to secure needed hybrids in the genus *Datura*.

Among the herbaceous Daturas there are ten species represented by their capsules in figure 3. They form a convenient group in which to study crossability and related phenomena. Figure 4 shows below an intact and an opened capsule of *D. ferox* resulting from selfing, and to the right an intact and an opened capsule which resulted from the cross between *D. ferox* and *D. meteloides*. It can be seen that the latter capsules are smaller

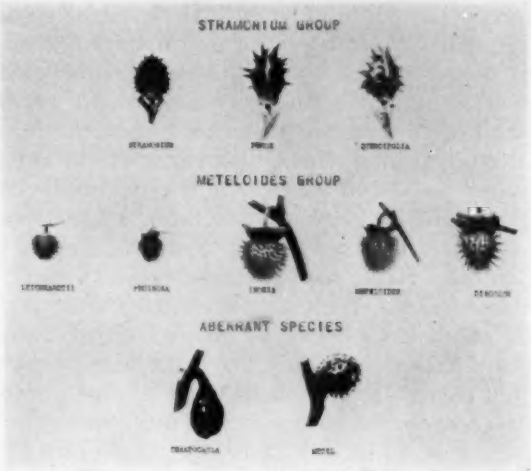


FIG. 3. Capsules of 10 herbaceous Daturas.

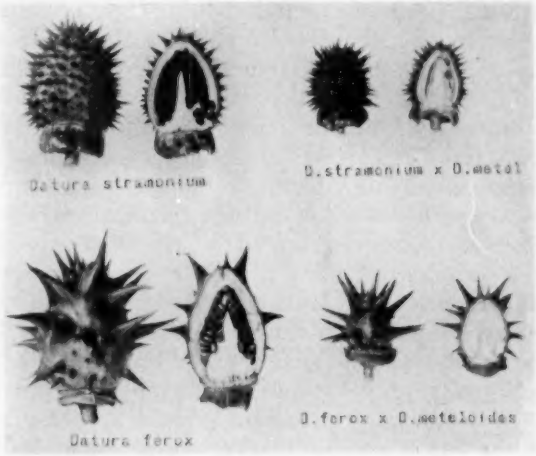


FIG. 4. Below, intact and opened capsule of *D. ferox* with similar capsules of the hybrid *D. ferox* × *D. meteloides*. Above, capsules of *D. stramonium* and of hybrid *D. stramonium* × *D. metel*.

and that they do not contain any seed-like bodies. This cross has never produced any viable seeds, nor dissectable embryos. On the upper row we have similarly selfed capsules of *D. stramonium* and capsules from the cross *D. stramonium* × *D. metel*. Two small seed-like bodies are seen in the opened crossed capsule. Such bodies sometimes, but not always, contain dissectable embryos. Thus the unopened capsule of the photograph was found upon dissection to have twenty-four such seed-like bodies which, however, were devoid of embryos. The opened capsule had a total of three such bodies but only one had an embryo and this embryo was dried and shrivelled and ob-

viously incapable of growth in artificial media. Frequently this cross will result in capsules without seed-like bodies and those with embryos are never abundant. As was pointed out earlier, fertilization occurs in this case but in the material studied in sections, development did not go beyond the 8-cell stage. It is only rarely that an embryo reaches a dissectable stage. Such sporadicity is found also in the formation of an occasional viable seed from the cross *D. metel* × *D. meteloides*. We made several hundred separate pollinations before we finally secured a single hybrid from this cross. The cause of sporadicity is not clear. It is probable that a large number of factors in the external and internal environment must all be in a favorable condition at the same time and spot in the ovary to allow the development of an embryo which under usual conditions is impossible. The clue to the problem will probably be found in a study of differences in the microenvironment rather than of differences in the macroenvironment more commonly considered.

If a pistil is not pollinated, it falls off within a few days. The growth of pollen tubes apparently brings in auxins which stimulate the growth of the capsules whether or not fertilization takes place and seeds are formed. Growth of capsules to a considerable size but without seed formation may be induced in Datura, as also in other forms, by treatment with various chemicals such as naphthalene acetic acid or indol-butyric acid.

Stages in development of normal embryos of *D. stramonium* are shown in figure 5. The one at the left is a proembryo six or seven days old and would measure around 0.1 mm. in diameter.

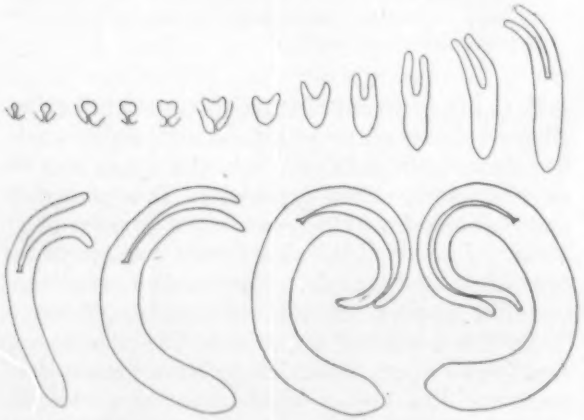


FIG. 5. Stages in development of embryos of *D. stramonium* from about a week old at upper left to month old mature embryos at lower right.

FIG. 6. Two microgreenhouses consisting of gelatine capsules used in micrografting dissected embryos.

The top soon becomes flattened and by the tenth day a pair of projections are developed which are destined to become the two cotyledons or seed leaves. By around the twelfth day the embryo is obviously heart-shaped. Further growth of the cotyledonary projections leads to what from its shape we have called the "torpedo" stage. Later the cotyledons increase greatly in size and are necessarily curved in adjustment to the available space within the seed coats. As was pointed out in last year's report, torpedo stages 1 mm. or more in diameter could be readily dissected out and cultivated on artificial media away from the parent plant. It was only by the addition of coconut milk, however, that the smaller embryos, down to 0.2 mm., could be cultured. Later we found malt extract as good as coconut milk in stimulating growth of the younger embryos.

We had earlier found considerable differences between reciprocal crosses. Thus *D. leichhardtii* forms viable hybrid seed when used as a female parent in crosses with most of the other species but has yielded hybrids with no other species when used as a pollen parent. The reverse is true of *D. discolor* which crosses readily with many other Daturas when used as a male but not when used as a female.

One of our graduate students, Miss Mary Sanders, is studying genetics of embryo development (10). She finds a similar difference in incompatible crosses in that it makes a difference regarding the stage at which development is arrested whether a given species is used as a male or a female. She finds further that hybrid embryos, whether they are the types which yield viable seed or those which become arrested before full development, are abnormal in comparison

INTERSPECIFIC CROSSES IN DATURA

♀ \ ♂	STRAM.	QUERCI.	FEROX	PRUNOSA	LEICH.	DISCOLOR	CERATO.	METELOID.	METEL.	INNOXIA
STRAMONIUM	£	X	X			X	[ED]	[ED]	ED	
QUERCIFOLIA	X	£	X			X				
FEROX	X		£			X	ED			
PRUNOSA				£			[ED]			
LEICHHARDTII	X	X	X	X	£	X	ED	X	ED	X
DISCOLOR	ED					£	ED			
CERATOCAULA						ED	£		ED	ED
METELOIDES						—	ED	£		
METEL	—					—	ED	XSP	£	XSP
INNOXIA	[ED]					[ED]	[ED]	X	[ED]	£

FIG. 7. Chart to show fertile hybrid seed (x) and dissected hybrid embryos (E D) secured from cross pollinations among the 10 species of Datura. [ED] indicates hybrid embryos which have been grown in soil. Females listed in left vertical column, males in upper horizontal row. The pound sterling sign with a cross indicates selfed seed. X S P indicates an extremely rare (sporadic) seed.

with embryos of a single species. When such embryos are grown in artificial cultures, their irregular development may involve the formation of multiple growing points, roots without shoots and shoots without roots. To overcome this latter barrier we have developed micrografting (3), whereby a gelatine capsule, coated with nail polish to prevent softening in contact with water, is used as a microgreenhouse. Micrografting has also been used to rescue embryos when the cultures have become infected with fungi. A couple of micrografts are shown in figure 6.

Figure 7 is a diagram which shows some of the progress we have made in securing hybrids among the ten species of Datura. If each species is used both as a male and as a female parent there are ninety combinations possible. Despite extensive tests we had secured viable hybrid seed (represented by crosses in the diagram) from only eighteen combinations. In twenty combinations, which have heretofore been considered incompatible, embryos have been dissected out and grown in culture. They are marked ED to indicate embryos dissected.

Further tests are being made and the chances are good that an increase will be secured in the incompatible combinations from which hybrids may be obtained by embryo culture. The species *D. quercifolia* we have not yet tested for dissectable hybrid embryos since, due to the difficulty of getting its seeds to germinate, we have had no plants of this species under cultivation for several years. We now find that the inhibition to germination resides in the seed coats and we are securing plants of *D. quercifolia* for hybridization by dissecting out the embryos from old seed and getting them to grow in cultures. A few of the combinations in figure 7 are marked with a minus sign to indicate that neither viable hybrid seed nor dissectable hybrid embryos appear possible. Owing to the rareness of success in some of the combinations, a rather large number of attempted crosses must be made before one is justified in listing a given combination as impossible.

D. ceratocaula is an aberrant, endemic species of Mexico which is adapted to growing in shallow ponds. Despite numerous attempts to cross it with other Daturas we had never succeeded in getting it to take part in formation of any viable hybrid seed. One of our graduate students, Miss Susanne McLean, has made a special study of the genetics of this species (8). She finds that when used as a pollen parent it will form hybrid embryos, which may be dissected out and grown in cultures, from crosses with all the other Datura species except *D. quercifolia* with which it has not yet been tested. As a female parent it has not been so extensively investigated but has already given dissectable hybrid embryos from a considerable number of new combinations. This species which was considered the only one which could form hybrids with no other Datura has, by the use of the dissection technique, become the one which bids fair to yield hybrids in the greatest number of combinations.

Figure 8 shows at the left a small plant of *D. inoxia*, at the right a plant of *D. ceratocaula* and in the center a hybrid between these two

FIG. 8. Plant of hybrid *D. inoxia* × *D. ceratocaula*, between parental species *D. inoxia* on left, *D. ceratocaula* on right.

species. The three plants are not entirely comparable in respect to conditions of growth but the hybrid is at least not inferior to its parents in vigor. The fact that *D. ceratocaula* will give hybrids by the dissection technique with all the other species of Datura with which it has been tested offers an opportunity to study the interaction of genes of different species. A discussion of the expression of the genes of *D. ceratocaula* in its different hybrids will be reserved for a later publication. It may be of interest, however, to report that Miss McLean has found certain characters of *ceratocaula* recessive in hybrids with one species and dominant in hybrids with others.

We have discussed unexpected success in securing hybrids with the aberrant species, *D. ceratocaula*. Still more unexpected is success in securing by the dissection method a hybrid between *D. inoxia* and a Tree Datura, *Brugmansia suaveolens*. This is an intergeneric hybrid if we accept the best taxonomic authority in placing the Tree Daturas in a separate genus from the herbaceous forms. A small plant of *D. inoxia* in flower is shown at the left in figure 8. Figure 9 shows a plant of *Brugmansia suaveolens*. During the past year it has flowered at only four different times. *D. inoxia* would flower continuously if it were prevented from forming capsules which stop flowering. The *Brugmansia* species is apparently self-incompatible and will not set capsules when self-pollinated. The hybrid shown in figure 10 is a vigorous plant. Its buds are pendant like those of its *Brugmansia* parent, but its mature flowers approach the erect position of the *D. inoxia* parent. It flowers abundantly and almost continuously. Its continued flowering, brought in from the *inoxia* parent, is a character the expression of which is made possible by failure to form capsules. Failure to set capsules might be due to inheritance of the self-incompatibility of the *Brugmansia* parent but is probably due primarily to sterility of the eggs and pollen grains of the hybrid. It has not yet been determined what the cause is of the sterility of this particular hybrid. If the sterility is due to its being a "mule" plant it should be possible to restore fertility by doubling the chromosome number. "Mule" plants will be discussed in the next section.

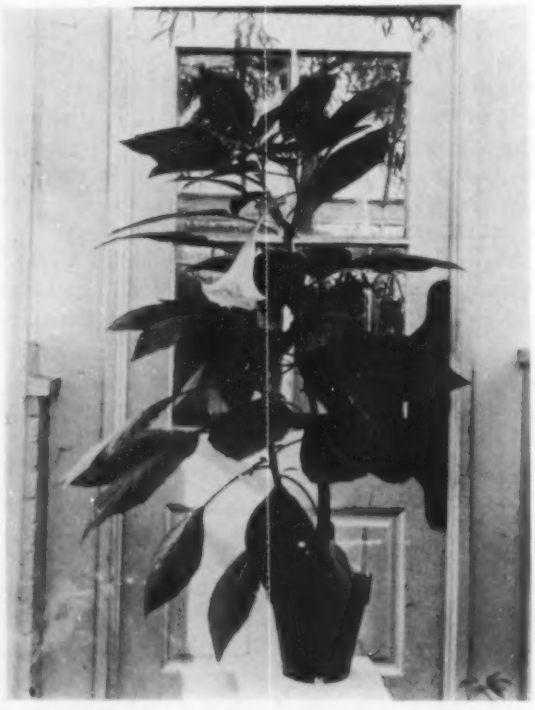


FIG. 9. Plant of *Brugmansia suaveolens*. Note single large pendant flower.

FIG. 10. Hybrid, *D. inoxia* × *Brugmansia suaveolens*. Note pendant buds and partially erect flowers.

13. RESULT OF CROSS MAY BE A STERILE "MULE" PLANT

"Mule" plants, like the sturdy mule, are sterile because the chromosomes of one parent are so unlike those of the other parent that they

FIG. 11. Flowers of hybrid *Nicotiana sylvestris* × *N. glutinosa*. Left, flower from sterile "mule" plant; right, flower from same hybrid rendered fertile by doubling chromosome number. Note plump anthers bursting with pollen of fertile flower in contrast with shrivelled anthers of sterile flower.

cannot mate and form pairs with them and without such pairing of the chromosomes there can be no sexual reproduction. If all the chromosomes of the hybrid "mules" are doubled each chromosome will have a duplicate from its own species with which it can pair and the plant will become a fertile "mule." Thus a barrier to the formation of a fertile hybrid will have been removed. The transformation of a sterile into a fertile "mule" plant has been established as a method of evolution of species in nature and of many of the best types of cultivated plants. Now that we have in the embryo dissection method a means of increasing the number of hybrids and in colchicine and other chemical treatments a ready means of doubling chromosome numbers, the production of fertile "mule" plants will doubtless be more frequently attempted. In view of their importance a few words in further explanation of "mule" plants may not be out of order.

Many of the hybrids within the genus *Nicotiana* are sterile. Figure 11 at the left shows a flower of the hybrid *N. glutinosa* × *N. sylvestris* kindly sent us by Dr. F. O. Holmes of the Rockefeller Institute at Princeton. This hybrid is sterile as can be seen from the photograph of its shrivelled pollen grains at the left in figure 12. Figure 11 at the right shows a flower of the same hybrid which has had its chromosome number doubled through treatment with colchicine (16). The flower has been increased in size especially the width of the throat; the anthers are bursting with pollen some of which has fallen on the corolla and the pollen grains have become plump as seen at the right in figure 12. No capsules are produced on the sterile hybrid but a branch with doubled chromosome number on the sterile plant will have capsules with abundant viable seed. Thus a pure-breeding new species has been synthesized in two steps: (*a*) the formation of a

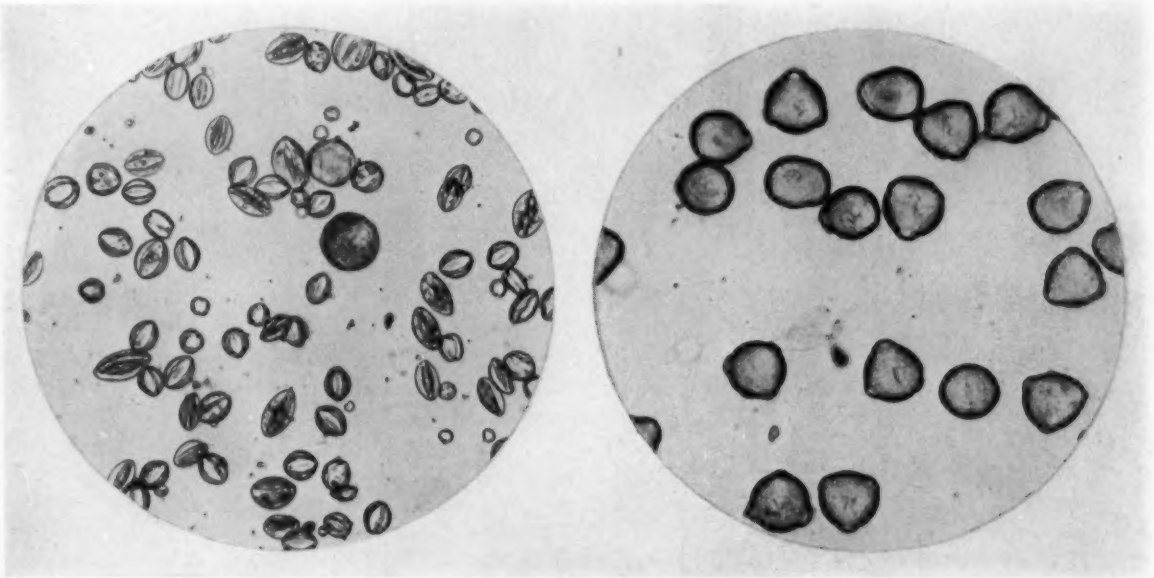


FIG. 12. Pollen of hybrid *N. sylvestris* × *N. glutinosa*. Left, pollen of sterile hybrid; right, pollen of hybrid after chromosome number doubled.

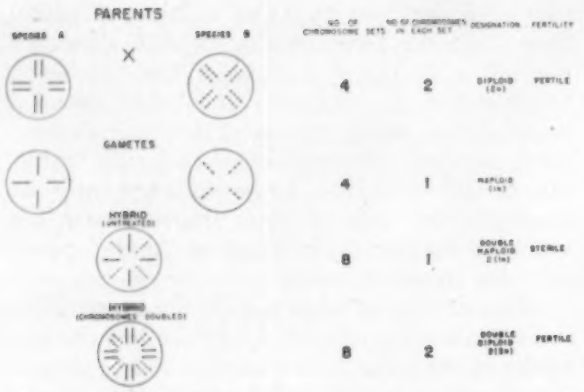


FIG. 13. Diagram to show chromosomal changes involved in the synthesis of fertile species hybrids.

sterile species hybrid or "mule" plant; (*b*) removal of the sterility by chromosome doubling. The process may be illustrated by the diagram of figure 13 in which it is assumed that two species, each with four chromosomes, are crossed to form a hybrid which is sterile since the chromosomes of the one species will not form pairs with those of the other. In the parental species the chromosomes are in pairs and are therefore diploid (2n). In the sex cells (gametes) the chromosomes are unpaired (1n). In the sterile hybrid the chromosomes are also unpaired and hence 1n or haploid, but since the chromosomal complexes of two species are involved it may be called a double haploid [2 (1n)]. This is an example of our sterile "mule" plants. When the chromosomal number is doubled there are two instead of only one of each kind of chromosomes and the type becomes a double diploid [2 (2n)]. Amphidiploid and less properly allotetraploid are terms which have been applied to sterile types which have been rendered fertile by chromosomal doubling. By similar procedure it may be possible to form multiple diploids in which the chromosomal complexes of several species are combined in a single type. In *Nicotiana* we have synthesized a triple diploid with chromosomal complexes from three species. With the known chromosomal incompatibilities in the genus *Nicotiana*, we have figured it should be possible

FIG. 14. Right, group of hybrid sunflowers; left, representative plants of the two parental species, and unbranched form of the cultivated sunflower and a silver-leaved branched species.

FIG. 15. Hybrid from the incompatible cross *D. inoxia* × *D. discolor*. Behind plant, Drs. Dorothy Hammond and Sophie Satina, the latter holding a box of culture vials similar to the one used for cultivation of the excised embryo from which the hybrid in the photograph had developed.

to produce a quintuple diploid involving five different species.

One of the characteristics expected of wide species crosses is hybrid vigor which is often marked. Figure 14 shows at the right a group of hybrid plants from a cross between a branched silver-leaved sunflower and a large-headed unbranched species. They grew so high that we had to use a tall stepladder in order to tie the paper bag on a flower head which may be seen in the photograph. Plants which were representative of the two parents were dug up and planted at the left before the picture was taken. Hybrid vigor, as is well known, is put to economic use in hybrid corn. It is an asset to be expected in wide species hybrids.

One of the most frequent questions we have been asked regarding our dissected hybrid embryos is whether they ever grow into normal plants or remain weaklings. It is true that they often grow extremely slowly in the nutrient agar and for a considerable time after being transplanted into soil. After they recover from this early period, however, they are fully as vigorous as their parents, if not more so. Figure 15 is a photograph of a hybrid, *D. inoxia* × *D. discolor*, secured from a dissected embryo, in front of Dr. Hammond and Dr. Satina who holds a box of embryo cultures. The hybrid is obviously of vigorous growth. Culturing dissected embryos from incompatible crosses should greatly increase the number of new hybrids some of which if sterile on account of incompatibility of chromosomes can be transformed into pure-breeding new species by chromosomal doubling.

It should be pointed out that not all species hybrids are sterile on account of chromosome incompatibility. None of the hybrids in the genus Datura are sterile for this reason although for other reasons 80 or 90 per cent of their pollen grains may be aborted. In consequence no fertile "mule" plants (or double diploids) have been

possible in Datura though the fertility may be increased somewhat in Datura hybrids by doubling their chromosome number.

A double diploid can probably not be secured from a hybrid which we have recently obtained by the dissection technique from a cross between a yellow flowered climbing Clematis (*C. tangutica*) and a blue-flowered non-climbing species (*C. heracleaefolia*) since it appears to have considerable good pollen.

DEVELOPMENT OF DESIRABLE RACES FROM NATIVE PLANTS

From the foregoing discussion of some of the ways in which barriers to crossability may be overcome through knowledge of the various mechanisms involved in fertilization and heredity, one might conclude that considerable technical knowledge would be a prerequisite to any attempts at plant improvement. Such knowledge would indeed help in directing the work but is far from essential. The old methods of selection are still profitable. An example will be given from our experience with the Yellow Daisy (*Rudbeckia hirta*), a common species of meadows and waste lands native to this country.

Figure 16 is a photograph with the flowers at left labelled "Native type from Northampton" and those at right labelled "Types from the Smith College Genetics Experiment Station."

Many of the flowers from our Experiment Station are over 6 inches in diameter and show various grades of doubleness as well as different types of form and arrangement of rays. Figure 17 is a close-up view in our experimental plots. Figures 18 to 20 are various arrangements of flowers in bouquets. The types shown in these photographs have been developed for doubleness of flowers. We have also developed a strain of single broad-rayed flowers of relatively large size and attractive form which have more or less strongly developed mahogany blotches at the bases of the rays, not well shown in the photograph of figure 20. The relative size of the flowers may be judged by the bricks of the background which are about eight inches long and two inches wide.

The types we have illustrated have been developed through well-known methods of plant breeding. Some thirty or more years ago at the University of Connecticut we became interested in the variations of the Yellow Daisy which we

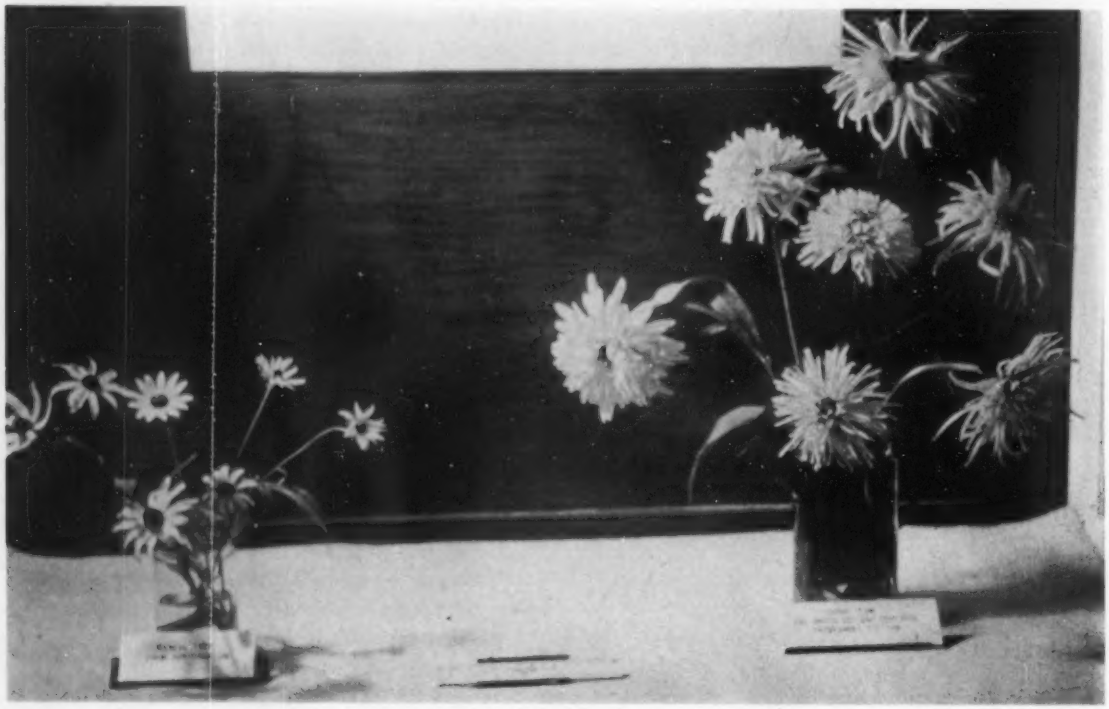


FIG. 16. Yellow Daisies (*Rudbeckia hirta*). Flowers at left labelled NATIVE TYPE FROM NORTHAMPTON; those at right labelled TYPES FROM SMITH COLLEGE GENETICS EXPERIMENT STATION

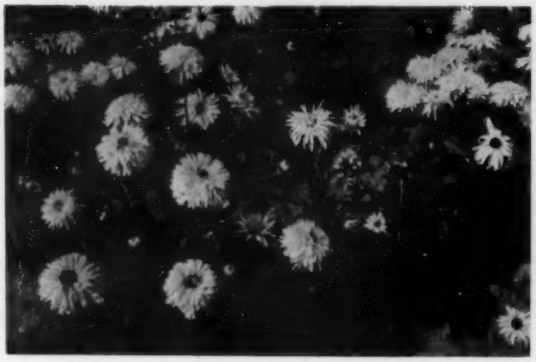


FIG. 17. Yellow Daisies. Plants in garden.

FIG. 19. Yellow Daisies. Doubles arranged in basket.

FIG. 18. Yellow Daisies. Doubles, semidoubles, and single arranged in vase.

FIG. 20. Yellow Daisies. Broad-rayed singles, some with mahogany patch at base of rays.

found growing abundantly in the adjacent meadows. These variations affected the color of the rays, their width, length, form, and number as well as many other characters of the flowers and habit of growth. In fact, we found variously expressed practically all the characters of flowers which one finds in modern Chrysanthemums or Dahlias. For some years we made the Yellow Daisy an object of genetic investigation, both in the region of Storrs, Connecticut, and also later in Cold Spring Harbor where we brought the work in 1915.

Each year during the summer season we visited many localities where the Yellow Daisies were growing and dug up plants which showed interesting types of floral structure or collected their seeds for later planting. In this way we got from nature a wide range of variations. The basal mahogany patch on the rays seen in some of the flowers of figure 20 we discovered was due to a dominant gene the expression of which was evidently modified by the action of other genes. Many of the characters we accentuated by hybridization. Apparently many genes are involved in characters which add to the attractiveness of the flowers. The number of rays, for example, we found could be increased by crossing together plants from different localities whose flowers had a relatively large number of rays. Ultimately by this method we secured flowers

that were fully double. We also found occasional double flowers in nature. In a similar way we were able to increase the length of rays by crossing long-rayed flowers together. By combining strains with double flowers with those that had long rays we were able to secure double flowers of increased size.

We soon found that our attempts to get races which were pure for any given characters resulted in greatly weakening their vigor and also in developing inter-class incompatibilities so that it was impossible to carry on inbreeding for many generations. In consequence we had to discontinue their use as a subject of genetic study. Later we recovered some of the more attractive types, largely from volunteer plants which came up near our old breeding plots, as well as from elsewhere, and took them into our home garden. The crossing program, because of the weakening effect of inbreeding and the interclass sterility that developed was discarded for a simpler method when we brought the plants into our own garden. We let the insects do the crossing for us and each year selected seeds from a few of the most attractive and vigorous plants. The following spring we would plant vigorous seedlings from these selected parents for our next generation. In this way we built up two large-flowering strains, one of double types and the other of single mahoganies, which we grew some distance apart to prevent their admixture by crossing. Later we doubled their chromosome number by treating their seeds with colchicine. The resulting plants showed among other changes a further increase in size of flowers, a deepening of the color of rays which we had also found in tetraploid (4n) yellow Cosmos, an increased brittleness of stems and a greater uniformity in the character of the progenies. Thus the offspring of a semi-double diploid (2n) Yellow Daisy include a considerable number of singles and also of full doubles which, however, produce few if any seed. The offspring of a tetraploid (4n) semi-double are chiefly intermediates and contain few singles and few full doubles. Further selection of the 4n plants will be necessary to eliminate certain undesirable characters connected with the doubled chromosome number.

We have given our experience with the Yellow Daisy as an example of what can be done with simple methods in utilizing the variations in nature of a native plant to build up attractive types for the garden. With more knowledge of how the plant solves its problems of growth, differentiation and reproduction, we have the alluring prospect of more power in the control of evolution and life processes.

REFERENCES

1. Blakeslee, A. F. 1941. Effect of induced polyploidy in plants. *Amer. Nat.* **75**: 117–135.
2. —— 1944. Smith College conference on plant embryo culture. *Science* **100** (2605): 497–498.
3. —— 1944. Micrografting, a method of securing seedlings from excised embryos which fail to develop roots. *Amer. Jour. Bot.* **31** (Oct.): 1s.
4. Blakeslee, A. F., and S. Satina. 1944. New hybrids from incompatible crosses in Datura through culture of excised embryos on malt media. *Science* **99** (2574): 331–334.
5. Buchholz, J. T., and A. F. Blakeslee. 1929. Pollen-tube growth in crosses between balanced chromosomal types of *Datura stramonium*. *Genetics* **14**: 538–568.
6. Buchholz, J. T., C. C. Doak, and A. F. Blakeslee. 1932. Control of gametophytic selection in Datura through shortening and splicing of styles. *Bull. Tor. Bot. Club* **59**: 109–118.
7. Buchholz, J. T., L. F. Williams, and A. F. Blakeslee. 1935. Pollen-tube growth of ten species of Datura in interspecific pollinations. *Proc. Nat. Acad. Sci.* **21**(12): 651–656.
8. McLean, S. 1944. New hybrids with the aberrant species, *Datura ceratocaula*, secured by embryo dissection. *Records Genetics Soc. Amer.* No. 13: 27.
9. Nebel, B. R., and M. L. Ruttle. 1937. Storage experiments with pollen of cultivated fruit trees. *Jour. Pomol. and Hort. Sci.* **14**(4): 347–359.
10. Sanders, M. 1944. Abnormalities in the development of interspecific hybrid embryos in Datura. *Amer. Jour. Bot.* **31**(8): 5s.
11. Sansome, E. R., S. Satina, and A. F. Blakeslee. 1942. Disintegration of ovules in tetraploid-diploid and in incompatible species crosses in Datura. *Bull. Tor. Bot. Club* **69**(6): 405–420.
12. Sanz, C. 1944. Pollen germination and pollen-tube growth of various species of *Solanaceae* and other families in pistils of *Datura stramonium*. *Amer. Jour. Bot.* **31**(8): 5s.
13. Satina, S., and A. F. Blakeslee. 1935. Fertilization in the incompatible cross *Datura stramonium* × *D. metel*. *Bull. Tor. Bot. Club* **62**: 301–312.
14. Satina, S. 1944. Periclinal chimeras in Datura in relation to development and structure (A) of the style and stigma (B) of calyx and corolla. *Amer. Jour. Bot.* **31**(8): 493–502.
15. Schaffner, J. H. 1925. The influence of the substratum on the percentage of sex reversal in winter-grown hemp. *Ohio Jour. Sci.* **25**(4): 172–176.
16. Warmke, H. E., and A. F. Blakeslee. 1939. Induction of simple and multiple polyploidy in *Nicotiana* by colchicine treatment. *Jour. Her.* **30**(10): 419–432.
17. Warmke, H. E., and A. F. Blakeslee. 1940. The establishment of a 4n dioecious race in *Melandrium*. *Amer. Jour. Bot.* **27**(9): 751–762.

INHERITANCE OF FACTORS INVOLVED IN ONE TYPE OF HETEROCARYOTIC VIGOR[1]

B. O. DODGE, MARY B. SCHMITT, AND ANITA APPEL

New York Botanical Garden

ABSTRACT

The growth rates of over 300 mycelia ("races") obtained by isolating each of the four spores from F_1 asci of the cross race $C_4 \times$ Dwarf 16, were determined and compared with the growth rate of the original heterocaryotic race C_4 + Dwarf 16. It was proved more conclusively that those factors which appear to govern the synthesis of the complementing growth substances resulting in heterocaryotic vigor are segregated at meiosis. These factors are then redistributed to the f_1 binucleate ascospores in such a way that mycelia from them in turn also carry two kinds of nuclei, not only as to their mating or sex-reaction types but also as to the complementing growth factors. In a number of asci the redistribution was such as to give two "double non-dwarfs" and two "double dwarfs." The former mycelia always grew with great vigor. The individual component races of each of some 140 different heterocaryotic mycelia representing 43 F_1 asci were also isolated. It was shown that the component races making up or constituting particular heterocaryons differ widely not only as to being either dwarf or non-dwarf but also as to their growth rates if both were non-dwarf. A number of non-dwarf component races were isolated which had growth rates practically equal to that of heterocaryotic races showing heterocaryotic vigor. While fertile heterocaryotic f_1 races from other crosses may grow slowly, the f_1 races from the cross $C_4 \times$ Dwarf 16 always grow with increased vigor over that of either C_4 or Dwarf 16. This is true whether or not the f_1 race being tested proves by the formation of asci with spores that it is fertile.

PRELIMINARY experiments[2,3] proved that when unisexual race Yellow Dwarf **16** of *Neurospora tetrasperma* derived from a small ascospore (fig. 1.V) was grown in culture with certain other slow-growing races a heterocaryotic condition of the mycelium was obtained through anastomoses and nuclear migration. The growth rate of the heterocaryotic mycelium was reported as far greater than that of either component race by itself, suggesting a phenomenon analogous to hybrid vigor. The problems involved were restated in the report of progress.[3] It was desired

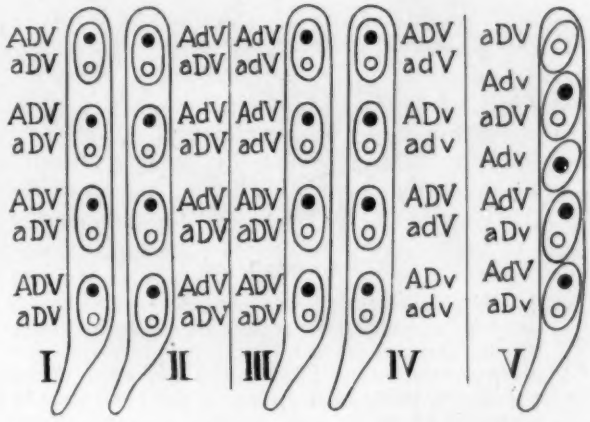


FIG. 1. *Neurospora tetrasperma*. Diagram showing the nuclear conditions in five different asci just after spore formation, but before the nuclei originally included in each spore have divided. A mature normal ascospore has four nuclei, two of each mating type, *A a*; *D* represents the wild type allele of the recessive lethal *d*; *V* represents the wild type allele of the "Dwarf" gene *v*.

I. Normal ascus showing that all four spores are alike as to the factors which we are considering, and heterocaryotic for mating types, but homocaryotic for normal spore delimitation and for vigorous vegetative growth. This ascus originally was heterozygous for mating type factors but homozygous for the other two pairs of factors.

II. The four spores are alike, heterocaryotic for mating types and for the pair, *D d*, but homocaryotic for *V*. Such spores give rise to mycelia which will develop fertile ascocarps whose asci delimit ascospores.

III. Ascus of the type from which races C_4 and C_8 were originally obtained. The upper two spores are homocaryotic for the recessive lethal *d*. Such spores as the upper two give rise to fertile mycelia which produce ascocarps with many asci but the asci abort without spore formation.

IV. An ascus which originally was heterozygous for all three pairs of factors which were so distributed that we have what we have called a "Double." Two spores, the first and third, will give rise to what we call "Double non-dwarf" mycelial growth, and two spores, second and fourth, will give rise to what we call "Double-dwarf" growths or races. (See our Group III and table 4.)

V. An ascus which was originally heterozygous for all three pairs of factors, just as were all the asci resulting from our matings of races C_4 and Dwarf **16**. This ascus happened to delimit five spores, the first and third spores are unisexual; the three binucleate spores are heterocaryotic for all three pairs of factors.

[1] This work was supported in part by a Grant-in-Aid from the American Philosophical Society. We are also indebted to Professor Marcus M. Rhoades and Professor F. J. Ryan for a critical reading of the manuscript and for numerous very helpful suggestions.

[2] Dodge, B. O., Heterocaryotic vigor in *Neurospora*, *Bull. Torrey Club* **69**: 75–91, 1942.

[3] Dodge, B. O., A study of the inheritance of factors for heterocaryotic vigor in *Neurospora tetrasperma*, *Year Book Amer. Philos. Soc.* 1942: 148–150, 1943.

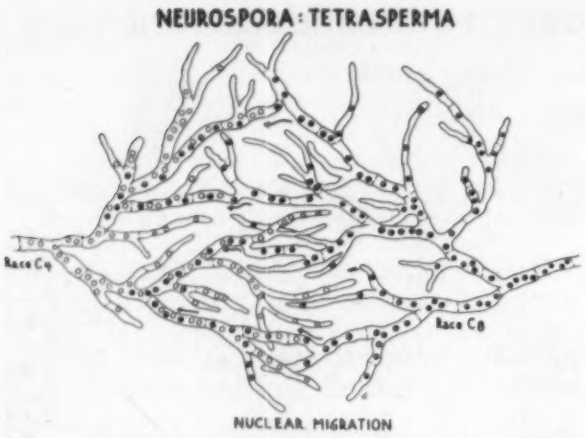


FIG. 2. Diagram showing how two races which are homocaryotic but which differ genetically can be combined through anastomoses and nuclear migration to form a heterocaryotic race. Black nuclei and white nuclei represent opposite mating types or any other pairs of alleles.

to test out more fully the manner of inheritance through the F_1 and F_2 hybrid asci of the factors or whatever it is that is responsible for this increased vigor of growth and production of conidia. In other words, following meiosis, how are these factors distributed among the eight nuclei which are eventually included in the four ascospores, two of opposite sex reaction or mating type in each spore? We are reporting here principally only on those phases of the work particularly concerned with the original problem, leaving until later a report on a number of the other interesting features met with in this work.

PROCEDURE

The races Yellow Dwarf **16**, C_4 and C_8 were described in the paper on heterocaryotic vigor.[2] Dwarf **16** produces few if any normal conidia under ordinary conditions, but breeding tests prove that its genotype is *aCD* and not *acD*. The lethal which prevents normal growth and which makes the race a dwarf, evidently "suppresses" (?) conidium formation. This dwarf is certainly not an "albino" or like other non-conidial races with which we have worked. Races C_4 and C_8 are of opposite mating types, *A* and *a*, and carry the same lethal gene *d*. The lethal *d* is recessive, causing ascus abortion only when the ascus is homozygous, *dd*. It also acts to "suppress" to a certain extent formation of conidia especially in race C_8 where it has certain other deleterious effects on the type of growth of the haploid vegetative stage. See figure 1 for explanatory illustration.

To obtain fertile ascocarps we mated races Yellow Dwarf **16** and C_4. Disregarding all other factors for the present, the fusion nuclei in the hybrid asci produced would all be alike *AaDd*. The asci normally would delimit four spores, each containing two nuclei of opposite mating type (fig. 1, II). Asci containing a full complement of mature spores were isolated under sterile conditions from crushed mounts and transferred to agar plates. The spores were then dissected out and isolated on the plate without regard to their positions in the ascus.[4, 5]

The plates, each now containing the four ascospores from the same ascus, were set aside over night to see if any of the spores germinated. If any did grow they were transferred, after which the remaining ones were given the heat treatment. If two or more spores from an ascus germinated, following such treatment, they were transferred to tubes of potato dextrose agar, one spore to each tube. The cultures were labeled to show the number of the ascus and the number of the spore. For example, the four cultures from ascus No. 25 would be labeled 25.1; 25.2; 25.3; 25.4, with the dates of transfer added. The spore number represents merely the order in which they happened to be transferred as noted above.

Some asci have only three spores, one "giant" spore and two of normal size. Spores from a number of such asci were isolated. Ascus No. 52 was of such a type. The three cultures were labeled 52.1; 52.2; 52.3, and it was recorded that spore No. 52.2 was a large spore. If cultures 52.1 and 52.3 were alike and different from 52.2 we assumed that 52.2 simply had its two kinds of nuclei in duplicate. Such an ascus was treated as a four-spored ascus for our particular purposes. In certain three-spored asci the giant

[4] While the place of a spore in an ascus of *N. tetrasperma* may possibly be determined by the manner of orientation of the nuclear spindles at the second division, and while a cross-over involving the factors for mating type may have an effect on spindle orientations, this has not been proved. In *Gelasinospora tetrasperma* the second division spindles are always placed one well above the other and parallel to the long axis of the ascus. Does this mean that those factors responsible for this orientation are involved in a cross-over at every meiosis? If so, then segregation of these factors would of necessity always occur in the second division. This question needs further study.

[5] Dodge, B. O., Spindle orientation and spore delimitation in *Gelasinospora tetrasperma*, *Cytologia*, Fujii Jubilee vol., 877–887, 1937.

spore gave a typical dwarf mycelium, showing that if four spores instead of three had been delimited we should have had two similar dwarf cultures and two similar non-dwarf cultures; or two Double dwarfs and two Double non-dwarfs. By "Doubles" we mean that the two races represented in each spore which is heterocaryotic for mating types is homocaryotic for wild type *V*, or for dwarf type *v*, i. e., *A V-a V; A V-a V; Av-av; Av-av.* (See figure 1, IV.) We obtained some fifty such sets of Doubles. Normally all four races would be bisexual. We proved out the dwarfs in only a few cases however.

If cultures were obtained from only three of the four spores in an ascus, these three cultures were at first set aside for future use, but were later discarded because they did not actually represent all the eight nuclei from that ascus. Theoretically three bisexual spores would, barring a mutation in the ascus, permit the determination of the genotypes of the two missing nuclei.

In order to learn whether the factors involved in heterocaryotic vigor were affected by those factors contributing to sterilities such as perithecium abortion, ascus abortion, and spore abortion, the cultures from a number of asci are grouped together below, so far as this could be done easily, to show common characters.

ASCUS GROUP I. NON-DOUBLES

A. All four cultures developed many perithecia, all of which matured many spores. Thirty-nine of this type were studied.

B. All four cultures developed many perithecia, but only two cultures produced many ascospores, the other two produced few if any ascospores. Only seven such cultures were noted. Evidently the factors for perithecium abortion are not identical with those factors which govern "fertilization." That is, even though two races may be of opposite haploid mating types as proved by the formation of large numbers of perithecia, yet other factors prevent in certain cases the formation of asci. Failure to form spores by a perithecium may also be due to ascus abortion which is quite another thing. Asci homozygous, *dd*, regularly abort without spore formation.

ASCUS GROUP II. NON-DOUBLES

Two of the four bisexual cultures developed abundant perithecia. Asci of this type are subdivided into two classes.

A. The two cultures with abundant perithecia produced many spores while the other two produced only a few or no spores. There were eleven asci of this type. Ascus No. 45 may have belonged here.

B. The cultures with *few* perithecia produced *many* ascospores in those few perithecia that did develop, while the other two cultures, both of which had *many* perithecia, produced *few* or no spores in these perithecia (just the reverse of those in class A). There were ten of this type. It should be noted that in none of the asci listed under classes "A" and "B" of Group II did all four cultures produce many ascospores in their perithecia.

C. The following asci of Group II were difficult to classify because all four cultures produced few or no spores: Nos. 28, 30, 36, 89, 100, 148, 173, 178, 183, 185, 191. Further study of such asci was not carried out. The perithecia were all semi-sterile. This could perhaps have been owing to the effects of recombinations of the various sterility factors operating, or even to some cultural irregularities so that two of the four cultures failed to develop according to type.

ASCUS GROUP III. DOUBLES

All asci in Group III gave rise to two cultures in which both components, which were isolated later, grew well, while the other two cultures represented dwarf races such that both component races were dwarfs and of opposite mating type. This could usually be determined either by the appearance of the Double-dwarf culture or by actual tests. Since it is a rather difficult matter to separate out the two dwarf components in such races we are considering here only the two Double non-dwarfs represented in each ascus. See figure 1, IV, for diagram.

A. 1. The two Double non-dwarfs both produced abundant perithecia with many ascospores. Twenty-four asci were of this class.

A. 2. The two Double non-dwarf cultures both developed many perithecia but these fruit bodies produced few or no ascospores. Here the factors for perithecium abortion, and not those which prevent fertilization or cause ascus abortion, were operating. We found only four asci of this type.

B. 1. The two Double non-dwarf cultures from each of four asci had few or no perithecia, but the few perithecia that did mature had many spores. Five were of this type.

B. 2. The two Double non-dwarfs from each

TABLE 1

AVERAGE 24-HOUR GROWTH RATES OF THE f_1 RACES FROM F_1 ASCI (DWARF 16 × C_4) INCLUDED IN GROUP I, A, ABOVE

All four cultures produced many perithecia and all perithecia produced many ascospores.

Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate
2.1	10.5	31.2	12.1	54.3	11.4	94.4	11.4	114.3[i]	3.9	138.3	11.8	155.4	10.6	192.1	10.8
2.2[a]	8.2	31.3	11.9	54.4	11.3	97.1	11.6		10.5	138.4	11.8	158.1[l]		192.2[m]	8.5
2.3	9.7	31.4	11.7	70.1	11.6	97.2	11.3	114.4	12.4	139.1	11.8	158.2	12.1		11.5
2.4	10.8	50.1	11.4	70.2[f]		97.3	11.4	121.1	11.5	139.2	12.1	158.3	11.8	192.3	11.5
12.1	11.7	50.2	11.9	70.3	11.8	97.4	11.6	121.2	11.9	139.3	12.1	180.1	11.8	192.4	11.3
12.2	11.5	50.3[c]	8.3	70.4	11.9	106.1[g]	10.4	121.3	11.8	139.4	12.2	180.2	11.9	193.1	12.2
12.3	11.7		10.1	79.1	10.8	106.2	10.8	121.4[j]		146.1	11.0	180.3	11.9	193.2	12.0
12.4	11.8	50.4	11.5	79.2	11.4	106.3	11.2	125.1	12.0	146.2	10.9	180.4	12.0	193.3	10.8
18.1	11.0	52.1	12.0	79.3	11.5	110.1	12.0	125.2	11.5	146.3	11.7	181.1	10.5	193.4	8.5
18.2	10.8	52.2[d]	11.8	79.4	11.5	110.2	12.0	125.3	11.7	146.4	11.6	181.2	10.5		12.0
18.3	10.5	52.3	11.9	86.1	11.5	110.3	11.8	125.4	11.1	147.1	12.0	181.3	10.0	194.1	11.7
18.4	10.7	53.1	11.7	86.2	11.6	110.4	11.9	131.1	12.0	147.2	12.0	181.4	10.2	194.2	11.7
19.1	10.7	53.2	11.6	86.3	11.2	111.1[h]	7.6	131.2[k]		147.3	12.0	189.1[m]	8.6	194.3	11.8
19.2	11.0	53.3	11.5	86.4	11.2	111.2	10.5	131.3	11.9	147.4	11.9		11.5	194.4	11.7
19.3[b]	—	53.4[e]	8.2	94.1	12.0	111.3	10.5	131.4	8.7	155.1	10.9	189.2	10.6	202.1	11.2
19.4	10.7	54.1	11.4	94.2	11.9	114.1	12.3	138.1	11.8	155.2	11.0	189.3	10.7	202.2	
31.1	11.7	54.2	11.3	94.3	11.9	114.2	12.2	138.2	11.9	155.3	11.2	189.4	11.2	202.3	10.3
														202.4	11.8

[a] Races 2.2 and 2.3 were probably not fully heterocaryotic, as an f_2 race from an ascospore from culture 2.2 grew at the rate 10.7, showing that the parent race, 2.2, carried the gene combination necessary for heterocaryotic vigor.

[b] Race 19.3 was unisexual by test. Its growth rate was not determined.

[c] Race 50.3 which grew at rate 8.3 on the first trial grew 10.1 at a later test. The heterocaryotic condition was then more complete.

[d] This was a 3-spored ascus. Spore 52.2 was a "giant" spore but the race grew no faster than did the other two races.

[e] 53.4. Probably the heterocaryotic condition was not complete in the inoculum.

[f] Race 70.2 was unisexual by test so did not carry the complementary factors.

[g] Ascus 106 was 3-spored. Spore 106.1 was very large, but growth from it was even slower than that from the normal spores.

[h] Spore 111.1 was a giant spore from a 3-spored ascus; even so the race grew as though the inoculum were not heterocaryotic.

[i] In the first test of race 114.3 it grew only at the rate 3.9. On a second test it grew 10.5 showing that the two kinds of nuclei were more equally distributed.

[j] Race 121.4 was a unisexual dwarf.

[k] Race 131.2 was a unisexual non-dwarf. Race 131.4 was bisexual; the inoculum was probably not fully heterocaryotic.

[l] Ascus 158 was 3-spored. Spore 158.1 was over-sized. This culture became contaminated.

[m] Race 189.1 grew at the rate 8.6, but an f_2 race from its ascospores grew 11.5 showing that the parent race had received the genes for heterocaryotic vigor, but the nuclei were unevenly distributed in the inoculum.

[n] Same as for race 189.1.

of six asci had few or no perithecia, but if a few perithecia did mature these had few or no spores.

GROWTH RATES OF f_1 RACES

The primary nuclei of F_1 asci are diploid, but the nuclei of the ascospores are haploid. The ascospores and cultures from F_1 asci are referred to as f_1 spores and f_1 races. When f_1 races are mated or crossed the asci developed will be F_2 asci and their spores and growth from them will be f_2 spores and f_2 races, and so on.

In determining growth rates we have used with slight modification the type of culture tubes described by Beadle and Tatum,[6] and by Ryan, Beadle, and Tatum.[7] For the most of the tests small agar plates were inoculated with conidia of a race and incubated until a good growth of mycelium had been obtained. Small blocks of agar bearing some of the growth were then transferred to the "racing tubes." A 2 per cent potato dextrose agar medium was used. The tubes

[6] Beadle, G. W., and E. L. Tatum, Genetic control of biochemical reactions in *Neurospora*, *Proc. Nat. Acad. Sci.* **27**: 499–506, 1941.

[7] Ryan, F. J., G. W. Beadle, and E. L. Tatum, The tube method of measuring the growth rate of *Neurospora*, *Amer. Jour. Bot.* **30**: 784–799, 1942.

were then placed in a 30° C. incubator over night. The next morning at a certain hour, the front of mycelial growth was marked with India ink. The point of growth reached at 4 o'clock in the afternoon was marked in the same way. We thus had two different twenty-four hour growth periods for comparison, or 9 A.M. to 9 A.M. and 4 P.M. to 4 P.M.

Tables 1–4 include the average daily growth rates in centimeters of the bisexual heterocaryotic non-dwarf races obtained from F_1 asci.

Foot-notes under each table explain certain irregularities encountered. Brackets [ ] enclosing a number indicates that that result was arrived at by interpolation.

It should be emphasized here that so long as it could be proved that an f_1 race was bisexual, that is, heterocaryotic for mating types, it was not important for our purposes to determine its genotype with respect to the genes *D* and *d*. As noted elsewhere this could have been determined without any uncertainty in each case by using numerous other tester races and following this with second generation analyses.

The results shown in table 1 indicate that all bisexual heterocaryotic f_1 races from the mating Dwarf **16** × $\mathbf{C_4}$ grew at a rate much greater than that of the unisexual homocaryotic parent races. They all showed heterocaryotic vigor. Race **16** being a dwarf grew only a fraction of a centimeter a day, but the other parent race $\mathbf{C_4}$ often grew 3 or 4 centimeters a day. See page 587 for the average growth rate of this race. In some cases the growth from an ascospore was unisexual as shown by tests. Unless the germinating ascospore itself is transferred the nuclei of one sex may not be carried over in the transfer. Furthermore, when one bisexual race has a growth rate much slower than that of the other three races from that ascus it is clearly because of unequal distribution of the two kinds of nuclei. This was proved in a number of cases by making transfers from regions showing several perithecia, or by growing f_2 ascospores. In general, if the parent f_1 bisexual race was not heterocaryotic for the complementing growth complexes the f_2 races could not very well show the usual increased vigor.

The senior author[8] pointed out that since race Arl. 10, through some sort of somatic mutation had become heterocaryotic as to those factors for conidial versus non-conidial races, conidia would be formed which would vary as to the number of nuclei of each kind which they would contain. One could, by plating out conidia, and selecting in each series conidia from that race producing the fewest conidia, obtain pure non-conidial races while others would be intermediate because they would be provided with different numbers of the different kinds of nuclei. That is, some cells or some conidia would contain, say, ten nuclei, each carrying the factor *C* for conidia while only two or three nuclei would carry the allele *c*. At that time, 1930, to quote,

> No other case has been reported in ascomycetes where a form derived through mutation or saltation has been bred or reproduced sexually to determine whether the mutation had involved factors which would be redistributed during the divisions of the nucleus of the mothercell.

[8] Dodge B. O., Breeding albinistic strains of the Monilia bread mold, *Mycologia* **32**: 9–38, 1930.

TABLE 2

AVERAGE 24-HOUR GROWTH RATES IN CM. PER DAY OF f_1 RACES FROM F_1 ASCI (DWARF **16** × $\mathbf{C_4}$) INCLUDED IN GROUP I, B, ABOVE

All four cultures from an ascus produced many perithecia but only two cultures produced many ascospores. The other two either produced sterile perithecia, that is, perithecia which aborted without producing asci, or a very few asci, as indicated by the presence in old perithecia of a few ascospores.

Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate
29.1	10.4	35.1[a]	9.2	35.4	10.4	59.2	10.8	66.3	10.2	76.3	11.1	115.3	11.3	171.4	11.0
29.2	10.7		11.6	45.1[b]	10.5	59.3	10.6	66.4	11.0	76.4	11.0	115.4	11.5	196.1	10.5
29.3	11.1	35.2	9.9	45.2	10.5	66.1	10.9	76.1	11.1	115.1	11.5	171.1	11.1	196.2	11.1
29.4	10.5	35.3	10.7	59.1[c]	11.4	66.2	11.1	76.2	11.0	115.2	11.8	171.2	11.9	196.3	11.2
												171.3	11.9	196.4	11.0

[a] 35.1 grew 9.2 cm. per day in first test, but 11.6 in a later test. Race 35.2 was not retested.

[b] Ascus 45 was 5-spored. Spore 45.3 was small and unisexual. Spore 45.4 was small and produced a unisexual dwarf race. 45.5 was of normal size but produced a Double dwarf race.

[c] No. 59.1 was a giant spore.

Table 2 shows that the growth rates are not materially affected by those factors which govern fertility of the perithecium in ascospore production. The point to be noted is that all these races showed increased vigor whether or not their mature perithecia produced ascospores in quantity.

The results recorded in table 3 further show that even though certain sterility factors prevent the formation of perithecia or prevent ascus development, the race shows heterocaryotic vigor provided the two kinds of nuclei in the mycelium are fairly evenly distributed.

Summarizing the results recorded in tables 1–4, it is clear that in all asci originating from the fusion of a nucleus from Dwarf **16** haploid parent with a nucleus from the haploid C_4 parent, there follows at meiosis a segregation of certain factors which have a complementing effect, directly or indirectly on growth rates. Each of the four ascospores delimited in an ascus receives two nuclei which are of opposite mating types. The same distribution of alleles representing other physiological or morphological characters can be expected only where there may be a close linkage between such factors and the factors for mating types *A* and *a*. There is something operating in such ascomycetes as *Neurospora tetrasperma* and *Gelasinospora tetrasperma* which normally brings two nuclei of opposite mating types into each spore before it is delimited. This attraction or force does not operate to control the distribution of other factors. For example, if we indicate the factor for dwarfness by *v* and the normal wild type allele by *V* it will be seen that all those asci listed a "Doubles" (table 4) show a distribution of *V* and *v* such that in every "Double" (bisexual) dwarf race the factor *v* is in both kinds of nuclei, that is, both kinds, considering mating types *A* and *a* only. The same holds for the "Double" (bisexual) non-dwarf races. The wild type gene *V* is carried by every nucleus regardless

TABLE 3

AVERAGE 24-HOUR GROWTH RATES IN CM. PER DAY OF f_1 RACES FROM F_1 ASCI (DWARF **16** × C_4) INCLUDED IN GROUP II, ABOVE

Two bisexual cultures had abundant perithecia, the other two cultures produced few or no perithecia. A. The two cultures with many perithecia produced many ascospores in each perithecium while few or no ascospores were produced in perithecia in the other two cultures. B. The two cultures with many perithecia produced few or no ascospores while the cultures with few perithecia produced many ascospores in the few perithecia that did mature. C. All four cultures in this class produced few or no ascospores, even though two cultures from each ascus set may have produced many sterile perithecia.

A				B				C	
Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate
5.1	11.0	102.1	10.1	3.1	11.5	41.1	10.6	89.1	10.8
5.2	10.3	102.2	10.3	3.2	11.9	41.2	11.0	89.2	10.8
5.3	10.7	102.3	10.5	3.3	11.5	41.3	10.4	89.3	10.6
5.4	10.4	102.4	10.4	3.4	11.8	41.4	11.3	89.4	11.1
58.1	11.0	115.1	11.3	17.1	10.7	43.1	10.8	148.1	9.4
58.2	10.4	115.2	11.8	17.2	10.6	43.2	10.5	148.2	10.9
58.3	10.2	115.3	11.3	17.3	11.4	43.3	11.0	148.3[c]	7.3
58.4	10.2	115.4	11.9	17.4	10.4	43.4	10.1	148.4	10.0
95.1[a]		117.1	11.3	22.1	11.1	44.1	10.7	183.1	10.8
95.2	11.7	117.2	11.5	22.2	11.5	44.2	10.8	183.2	10.9
95.3		117.3[b]		22.3	10.5	44.3	10.0	183.3[d]	7.0
96.1	10.6	117.4	11.0	22.4	10.5	44.4	10.9	183.4	11.3
96.2	11.4	176.1	11.4	26.1	10.6	101.1	10.8	191.1[e]	4.5
96.3	11.3	176.2	11.2	26.2	10.7	101.2	10.0	191.2	11.0
96.4	11.7	176.3	11.0	26.3	10.3	101.3	11.1	191.3	
		176.4	11.2	26.4	11.0	101.4	10.9	191.4	11.2
								191.5	11.3

[a] 95.1. Giant spore produced dwarf race. 95.2 and 95.3 were spores of normal size. Growth rate of 95.3 not determined.

[b] 117.3, unisexual dwarf race.

[c,d] 148.3 and 183.3, probably not evenly heterocaryotic.

[e] 191.1. A small unisexual spore.
191.3. A unisexual dwarf race.
If ascus 191 had been 4-spored, 191.1 and 191.3 would have been combined and not separated.

TABLE 4

AVERAGE 24-HOUR GROWTH RATES IN CM. PER DAY OF THE TWO "DOUBLE NON-DWARF" f_1 RACES FROM F_1 ASCI (DWARF 16 × C_4) RECORDED IN GROUP III, ABOVE

Races from these asci are designated "Double non-dwarfs" and "Double dwarfs." See figure 1, IV. There are two of each kind in a set. Growth rates of the dwarfs were not determined.

A. Both Double non-dwarfs produced many perithecia. These races are further sub-divided: (A.1) both cultures matured many ascospores; (A.2) both cultures produced few or no ascospores.

B. Both Double non-dwarfs produced few or no perithecia. These are further sub-divided: (B.1) both cultures produced many ascospores in the few perithecia that did mature; (B.2) few or no ascospores were formed. Even though no f_2 ascospores are matured the growth rates of the f_1 races can be determined because *growth rate* is a characteristic of the *vegetative* stage.

A.1						A.2		B.1	
Race	Rate	Race	Rate	Race	Rate	Race	Rate	Race	Rate
47.1[a]	8.5	116.1	11.5	153.3	12.1	34.1	10.5	27.1	10.3
47.2	11.0	116.3[b]	13.5	154.1	11.0	34.3	10.1	27.2	10.8
60.1	11.6	119.1	11.1	154.2	11.5	42.2	10.5	39.1	10.5
60.2	11.7	119.4	11.0	156.1	11.0	42.3	10.6	39.4	10.2
69.2	11.3	120.1	12.4	156.4	11.0	78.1	11.7	93.1	10.6
69.3	11.1	120.4	11.4	166.1	11.2	78.2	11.1	93.3	10.7
80.2	11.3	122.1[c]	11.1	166.4	11.1	149.1	11.9	118.1[e]	6.0
80.4	11.4	122.2		179.1	11.8	149.2	11.8	118.2	—
91.2	12.0	124.3	11.5	179.2	12.2				
91.4	11.5	124.4	11.5	201.1	11.5			B.2	
98.1	11.5	136.3[d]		201.4	11.7				
98.2	11.3	136.4	11.2	204.2	11.6			157.2	9.8
		153.1	12.0	204.3	11.7			157.3	10.6

[a] 47.1 proved to be unisexual.

[b] 116.3 probably some "slip" in growth rate.

[c] 122.1 and 122.2 were both giant spores from a 2-spored ascus. 122.2 gave a Double dwarf race.

[d] 136.3 was a Double non-dwarf which was at first slow in becoming evenly heterocaryotic. 136.4 was a Double non-dwarf which grew vigorously from the start.

[e] 118.1 and 118.2 were both giant spores from a 2-spored ascus. 118.1 was unisexual as transferred. 118.2 produced a Double dwarf race.

of its mating type. Therefore we can say that the four bisexual f_1 races derived from the four spores from an ascus classed as a "Double" would be (1) *AV-aV;* (2) *AV-aV*, both alike and non-dwarfs; (3) *Av-av;* (4) *Av-av*, both alike and dwarfs. This proves that a cross-over had occurred because there are four kinds of haploid races represented in the progeny from a single ascus mother cell. If no cross-over occurs there will be, barring a mutation during the nuclear divisions in the ascus, only two kinds of nuclei, which means only two kinds of races. This is a fundamental principle now very generally recognized by cytogeneticists.

Our results indicate that the heterocaryotic vigor reported here is the resultant of the effects of the additions of complementing growth substances now synthesized by the heterocaryotic mycelium in each case. This does not mean that the physiological processes involved are necessarily limited to the idea of a single pair of genes controlling the synthesis of all the necessary growth substances accounting for the increased vigor reported here. Our main interest was, of course, to determine to what extent the factors governing this vigor are heritable. Nevertheless it is evident from our comments in connection with Ascus Group I–III that certain sterility factors were interfering with the development of ascocarps and that other sterility factors prevented the formation of asci even when abundant ascocarps were developed.

Malloch[9] analyzed in great detail results obtained by growing f_1 haploid progeny cultures from an irradiated bisexual ascospore. Whether or not we were dealing also with the effects of the same or similar sterility factors which he discusses can best be determined when he isolates the two components of each of the four ascospores in each ascus analyzed. We shall now indicate how this has been done in a number of the asci which we analyzed.

[9] Malloch, W. S., The inheritance of induced mutations in *Neurospora tetrasperma*, *Mycologia* **34**: 325–347, 1942.

ISOLATING UNISEXUAL COMPONENTS

As noted previously, it is clear that more light will be thrown on the questions raised above if we analyze a number of asci from each of the groups treated in tables 1–4 by isolating the unisexual components making up the four bisexual f_1 races from each ascus. Dodge[10] has shown that the two components of a bisexual race can be separated by isolating the smaller more slowly growing conidia. The same method can be employed to separate the various components of any heterocaryotic race, even though the components may be of the same sex. When a race is a Double dwarf the components can be separated by roughly shaking small tufts of mycelial growth in a test tube containing a small amount of sterile water, then spreading the contents thinly over the surface of a hard-agar plate. The fragments must be allowed to grow for several days before making the isolations, choosing the ones showing only a little growth. This technique is more apt to result in the isolation of unisexual dwarfs instead of bisexual dwarfs.

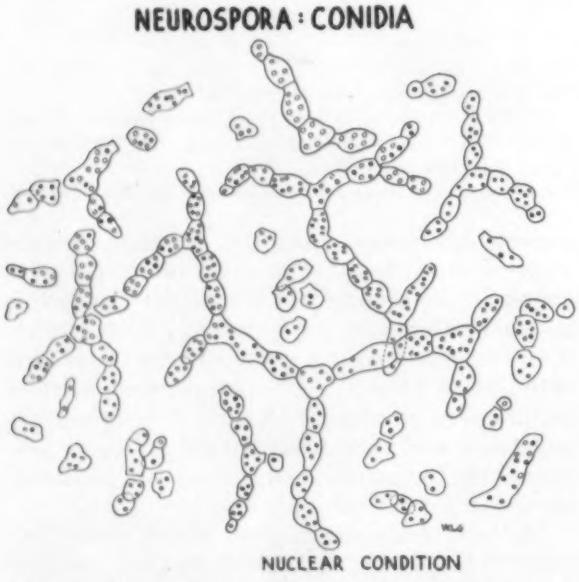


FIG. 3. Diagram showing that the cells making up the chains of conidia of *Neurospora* are as a rule multinucleate. If the race is heterocaryotic for mating types or for any other factors the components can be isolated by plating out the conidia, preferably choosing the smaller and more slowly growing ones. It often happens that conidia cut off have become homocaryotic through accidental separation of the two kinds of nuclei.

[10] Dodge, B. O., Unisexual conidia from bisexual mycelia, *Mycologia* **20**: 226–239, 1928.

Ordinarily each of our four f_1 bisexual races will always include one unisexual "dwarf" nucleus, except of course in case of the Double non-dwarfs of Group III and table 4. In such cases both components of the Double non-dwarfs will be non-dwarfs and of opposite mating types. We isolated the eight unisexual components from over forty asci, among them there were twelve asci which belonged to the "Double" sets of Group III.

Since the third nuclear division in an ascus is always equational the eight components represent only four pairs, the members of a pair being exactly alike. At most, and then only in case of a cross-over, there can be only four kinds of nuclei or potential gametes in an ascus.

When a bisexual race is composed of one non-dwarf and one dwarf we have designated the non-dwarf by the subscript $_1$ and the dwarf by subscript $_2$. For example, the eight components represented in ascus No. 12 would be 12.1_1, 12.1_2; 12.2_1, 12.2_2; 12.3_1, 12.3_2; 12.4_1, 12.4_2. The components of a Double non-dwarf race such as 47.1 are designated as 47.1_{1a} and 47.1_{1b}. Neither component is a dwarf. No. 47.3 is a Double dwarf. Its components are designated as 47.3_{2a} and 47.3_{2b}. Both are dwarfs but they are of opposite mating type.

The growth rates of unisexual homocaryotic component races were determined in the same way as were growth rates of bisexual heterocaryotic races. For comparison the growth rates of the four heterocaryotic races from each ascus are given again in table 5 along with the growth rates of their non-dwarf homocaryotic component races.

We would like to have included in table 5 under a heading "Genotype" the genotypes of the individual component races isolated, although, as previously stated, owing to certain troublesome incompatibility and sterility factors which either prevented ascocarp formation or prevented the formation of asci even though the ascocarps themselves developed, we could not always be absolutely certain that the determination of *d* was correct. In testing a race for its mating type and for the genes *D* and *d* it was customary to grow the race in culture with races C_4 and C_8, both of which carry *d* and they are of opposite mating type. The race to be tested ordinarily would fruit with one or the other of the tester races but sometimes both combinations remained sterile, or if ascocarps were produced in the mating with one of the testers, asci might not develop

TABLE 5

THE AVERAGE 24-HOUR GROWTH RATES IN CM. PER DAY OF EACH OF THE FOUR f_1 BISEXUAL RACES DERIVED FROM SPORES FROM F_1 ASCI (DWARF 16 × C_4), ALSO THE GROWTH RATES OF THE NON-DWARF (*V*) UNISEXUAL COMPONENT OF EACH RACE (DESIGNATED BY THE SUBSCRIPT 1 OR, WHERE BOTH COMPONENTS ARE NON-DWARFS, BY 1_a AND 1_b)

Growth rates of the dwarf race components were not determined. In the column headed "Race" the number at the left of the decimal point refers to the number of the particular ascus.

CULTURE		UNISEXUAL NON-DWARF COMPONENT		CULTURE		UNISEXUAL NON-DWARF COMPONENT	
Race	Rate	Race	Rate	Race	Rate	Race	Rate
3.1	11.5	3.1_1	2.5	69,3	11.4	69.3_{1a}	7.1
3.2	11.5	3.2_1	9.2	69.3	11.4	69.3_{1b}	8.6
3.3	11.5	3.3_1	1.5	78.1	11.6	78.1_{1a}	7.6
3.4	11.8	3.4_1	9.1	78.1	11.6	78.1_{1b}	4.0
5.1	11	5.1_1	7.8	78.2	11.2	78.2_{1a}	7.0
5.2	11	5.2_1	7.8	78.2	11.2	78.2_{1b}	5.0
5.3	10.7	5.3_1	7.3	79.1	10.8	79.1_1	6.2
5.4	10.9	5.4_1	7.7	79.2	11.4	79.2_1	6.2
18.1	11	18.1_1	8.7	79.3	11.5	79.3_1	9.5
18.2	10.8	18.2_1	[8.7]	79.4	11.3	79.4_1	9.0
18.3	10.5	18.3_1	3.0	80.2	11.3	80.2_{1a}	[6.3]
18.4	10.6	18.4_1	[3.0]	80.2	11.3	80.2_{1b}	[9.4]
26.1	10.3	26.1_1	1.7	80.4	11.5	80.4_{1a}	6.3
26.2	10.7	26.2_1	1.0	80.4	11.5	80.4_{1b}	9.4
26.3	10.3	26.3_1	10.4	91.2	12	91.2_{1a}	10.4
26.4	11.0	26.4_1	10.2	91.2	12	91.2_{1b}	2.7
31.1	11.8	31.1_1	2.5	91.4	11.5	91.4_{1a}	10.8
31.2	12.1	31.2_1	9.1	91.4	11.5	91.4_{1b}	2.5
31.3	11.9	31.3_1	9.0	96.1	10.5	96.1_1	8.4
31.4	11.7	31.4_1	2.5	96.2	11.4	96.2_1	1.2
41.1	10.6	41.1_1	10.2	96.3	11.3	96.3_1	8.5
41.2	11.0	41.2_1	10.6	96.4	11.7	96.4_1	1.7
41.3	10.4	41.3_1	10.4	98.1	10.9	98.1_{1a}	6.6
41.4	11.3	41.4_1	10.7	98.1	10.9	98.1_{1b}	—
44.1	10.7	44.1_1	5.6	98.2	11.3	98.2_{1a}	6.7
44.2	10.8	44.2_1	5.3	98.2	11.3	98.2_{1b}	8.3
44.3	10.0	44.3_1	5.6	101.1	10.8	101.1_1	2.1
44.4	10.9	44.4_1	5.4	101.2	10.8	101.2_1	2.5
50.1	11.4	50.1_1	6.9	101.3	11.1	101.3_1	2.7
50.2	11.8	50.2_1	7.5	101.4	10.9	101.4_1	2.8
50.3	10.1	50.3_1	7.5	102.1	10.1	102.1_1	5.8
50.4	11.5	50.4_1	7.0	102.2	10.5	102.2_1	5.6
52.1	12	52.1_1	10.9	102.3	10.6	102.3_1	5.7
52.2	11.8	52.2_1	2.1	102.4	10.0	102.4_1	6.5
52.3	11.9	52.3_1	10.0	110.1	12.0	110.1_1	2.7
[52.4]	11.8	52.4_1	2.1	110.2	12.0	110.2_1	8.7
58.1	11	58.1_1	4.9	110.3	11.8	110.3_1	8.7
58.2	10.4	58.2_1	7.4	110.4	11.7	110.4_1	1.7
58.3	10.2	58.3_1	7.6	112.1	2.4[b]	112.1_1	[2.4]
58.4	10.2	58.4_1	5.5	112.2	9.0	112.2_1	9.0
63.1[a]	11.0	—	—	112.3	2.6	112.3_1	2.6
63.2	Dwarf	—	—	112.4	9.1	112.4_1	9.1
63.3	Dwarf	—	—	114.1	12.3	114.1_1	10.9
63.4	10.7	—	—	114.2	12.3	114.2_1	11.3
63.5	10.6	—	—	114.3	10.5	114.3_1	1.5
69.2	11.5	69.2_{1a}	7.2	114.4	12.4	114.4_1	[1.5]
69.2	11.4	69.2_{1b}	8.6	115.1	11.5	115.1_1	1.3

[a] Ascus 63 was a 5-spored ascus; 61.1, 63.4 and 63.5 appeared to be unisexual after transfer, the dwarf component in each case was lost. Growth rates of the non-dwarfs indicate either a heterocaryotic condition or a recombination so that the complementing factors for increased vigor were brought into each nucleus.

[b] Ascus 112 had four spores which were proved by tests to be unisexual so that 112.1 and 112.1_1 are identical as were the others, i. e., 112.2 = 112.2_1, etc.

TABLE 5 (*Continued*)

Culture		Unisexual non-dwarf Component		Culture		Unisexual non-dwarf Component	
Race	Rate	Race	Rate	Race	Rate	Race	Rate
115.2	11.8	115.2_1	8.8	147.3	12.0	147.3_1	8.1
115.3	11.4	115.3_1	1.2	147.4	11.9	147.4_1	6.5
115.4	11.9	115.4_1	8.7	149.1	12.0	149.1_{1a}	10.7
116.1	11.5	116.1_{1a}	6.3	149.1	12.0	149.1_{1b}	3.4
116.1	11.5	116.1_{1b}	9.7	149.2	11.8	149.2_{1a}	[10.7]
116.3	13.3?	116.3_{1a}	6.3	149.2	11.8	149.2_{1b}	2.5
116.3	13.3?	116.3_{1b}	[9.7]	154.1	11.1	154.1_{1a}	8.7
119.1	11.1	119.1_{1a}	6.6	154.1	11.1	154.1_{1b}	6.6
119.1	11.1	119.1_{1b}	6.5	154.2	11.6	154.2_{1a}	8.9
119.4	11.0	119.4_{1a}	6.7	154.2	11.6	154.2_{1b}	6.6
119.4	11.0	119.4_{1b}	6.7	155.1	10.9	155.1_1	8.2
121.1	11.5	121.1_1	1.6	155.2	10.8	155.2_1	8.3
121.2	11.9	121.2_1	1.4	155.3	11.2	155.3_1	[8.3]
121.3	11.8	121.3_1	2.1	155.4	10.6	155.4_1	8.2
121.4[c]	[11.7]	[121.4_1]	[2.1]	156.1	11.0	156.1_{1a}	7.0
122.1[d]	11.1	122.1_{1a}	10.3	156.1	11.0	156.1_{1b}	7.4
122.1	11.1	122.1_{1b}	2.3	156.4	11.0	156.4_{1a}	[7.0]
125.1	11.5	125.1_1	2.4	156.4	11.0	156.4_{1b}	[7.4]
125.2	11.7	125.2_1	2.0	157.2	10.5	157.2_{1a}	10.7
125.3	11.2	125.3_1	2.3	157.2	10.5	157.2_{1b}	1.0
125.4	11.1	125.4_1	2.4	157.3	10.6	157.3_{1a}	10.7
131.1	12.0	131.1_1	8.7	157.3	10.6	157.3_{1b}	1.1
131.2[e]	[8.6]	[131.2_1]	[3.0]	171.1	11.2	171.1_1	9.9
131.3	12.0	131.3_1	8.7	171.2	10.9	171.2_1	9.8
131.4	8.6	131.4_1	3.0	171.3	11.0	171.3_1	2.0
136.3	[10.6]	136.3_{1a}	1.8	171.4	11.0	171.4_1	2.0
136.3	[10.6]	136.3_{1b}	[7.6]	181.1	10.5	181.1_1	5.4
136.4	10.6	136.4_{1a}	7.6	181.2	10.5	181.2_1	5.6
136.4	10.6	136.4_{1b}	1.7	181.3	10.0	181.3_1	6.3
138.1	11.8	138.1_1	7.6	181.4	10.2	181.4_1	6.3
138.2	11.9	138.2_1	2.0	183.1	10.8	183.1_1	7.1
138.3	11.8	138.3_1	7.6	183.2	11.0	183.2_1	4.4
138.4	11.9	138.4_1	3.2	183.3	6.9	183.3_1	6.9
139.1	11.8	139.1_1	9.3	183.4	11.2	183.4_1	4.4
139.2	12.1	139.2_1	9.5	194.1	11.7	194.1_1	2.0
139.3	12.1	139.3_1	1.3	194.2	11.7	194.2_1	10.8
139.4	12.2	139.4_1	1.4	194.3	11.8	194.3_1	2.2
147.1	12.0	147.1_1	7.3	194.4	11.9	194.4_1	10.7
147.2	12.0	147.2_1	6.1				

[c] Race 121.4 was a unisexual dwarf, the companion non-dwarf had been lost. Its growth rate is interpolated.

[d] Ascus 122 contained two giant spores, one of which, 122.2, gave a dwarf mycelium.

[e] Race 131.2 was a unisexual dwarf. We have interpolated its absent mate 131.2_1 with the same growth rate as that of 131.4_1. Race 131.3 grew only 8.6, no doubt because not evenly heterocaryotic. Not retested.

owing to sterility factors. We assumed that if ascospores were formed in any case the race being tested carried the factor *D* and not *d*. If no ascospores could be found in crushed mounts or if few asci without spores developed we assumed that the race being tested carried the lethal *d*. There can be no question that such a procedure must have led to a few errors in genotype determination and therefore the genotypes were not recorded in table 5. If our project had called for a genetic interpretation of the results we could have checked the more doubtful determinations of *d* by using other tester races and following this up through second generation progeny as noted elsewhere.

Races 98.1 and 98.2 were Double non-dwarfs which grew about 11 cm. per day. Both races produced a fluffy orange-colored aerial growth with conidia. These races were very fertile, ascospores being developed abundantly. Races

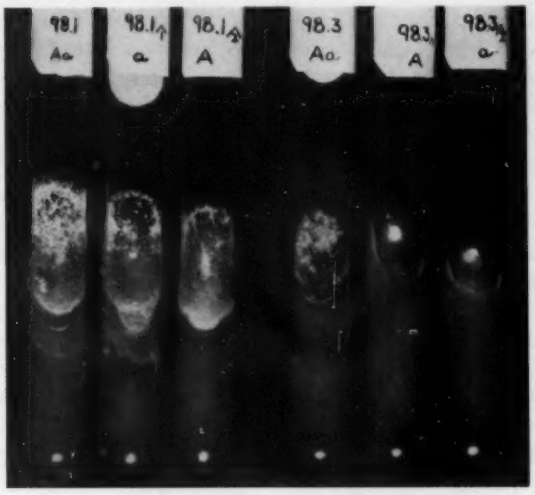


FIG. 4. Ascus No. 98 was an example of ascus sets which were placed in Group III, A.1. "Doubles." There were in each case two double non-dwarf races (here 98.1 and 98.2) and two double dwarfs (here, 98.3 and 98.4). Only one race of each kind is shown in this figure, namely, 98.1 and 98.3. Cultures of the two components are shown at the right in each case. Culture 98.3, a double dwarf, shows some heterocaryotic vigor. See text below for further discussion of this set.

98.3 and 98.4 from the same ascus No. 98 were Double dwarfs. They grew rather well for dwarfs, and each one produced a few pinkish conidia. Only one race of each kind of "Double" is shown in figure 4 above. The two non-dwarf component races of race 98.1 were labeled 98.1_1 and 98.1_2, instead of 98.1_{1a} and 98.1_{1b} as in table 5. Component race 98.1_1, mating type *a*, produced a fluffy aerial growth with conidia. It grew only about 6.6 cm. per day. Component race 98.1_2, mating type *A*, grew about 6.5 cm. per day and made a smooth velvety surface growth and some orange-colored conidia. When these slowly growing components were reunited as they had originally been in race 98.1 their growth rate was increased to over 11 cm. per day, thus showing true heterocaryotic vigor.

In culture the components 98.3_1 and 98.3_2 of the Double dwarf race No. 98.3 grew very slowly by themselves but when combined heterocaryotically (fig. 4, culture 98.3) there was a considerable increase in growth rate. One can very often distinguish a Double dwarf from a homocaryotic or single dwarf by the more vigorous growth of the former. This would prove that, in some cases at least, two dwarf races may furnish certain complementing growth factors to give heterocaryotic vigor. Nevertheless, such growth will be slow. We could say that the factor *v* for dwarfness carried by both dwarf components is not rendered wholly imperative. Those who would speak of a "*Dominance*" of *v* in this type of heterocaryosis would have much to explain.

Ascus set No. 41 represents a special case but it was placed in our Group II.B. The non-dwarf component races grew about as vigorously as did their heterocaryotic combination races. For example (see fig. 5) race 41.1 grew 10.6 cm. per day and its non-dwarf component 41.1_1 grew 10.2 cm. per day. Race 41.2 grew about 11 cm. per day, while its non-dwarf component 41.2_1 grew 10.6 cm. per day, there must have been a redistribution of complementing growth factors so that now each of the four non-dwarf homocaryotic component races grew vigorously by itself. In other words, instead of the necessary different kinds of complementing growth factors being distributed in two different kinds of haploid nuclei, they are now all included in every haploid nucleus. The difference in the growth rate of the heterocaryotic race 41.1 and that of each of its homocaryotic component races is slight. Non-dwarf component race 41.1_1 and dwarf component race 41.1_2 combined in heterocaryosis do

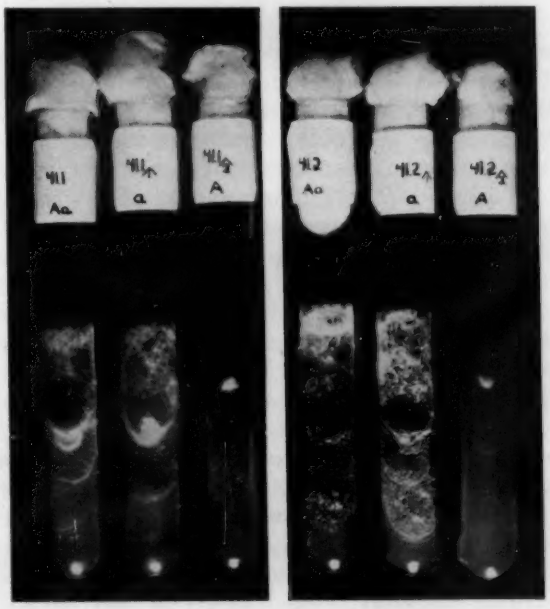


FIG. 5. Ascus No. 41 represents such ascus types as were placed in Group II, B. This ascus, however, illustrates a special case such as may be found in any of the other groups as well. Both non-dwarf component races grew about as vigorously as did their heterocaryotic combination race. Compare with ascus set 44 and see below in the text for further comment.

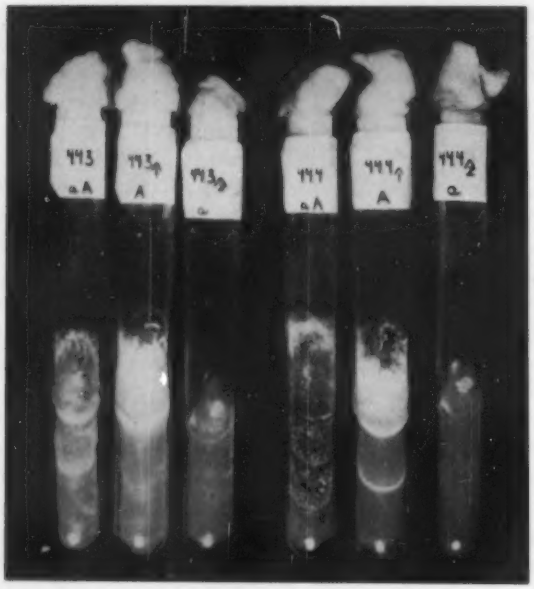


FIG. 6. Superficially cultures representing the four heterocaryotic races derived from ascus No. 44 looked much like those from ascus No. 41 shown in figure 5. The non-dwarf component races 44.3_1 and 44.4_1 grew slowly, but when each was combined with its dwarf companion component, the heterocaryotic races grew vigorously. See below in text for further discussion.

not result in noticeable heterocaryotic vigor. The distribution of the complementing growth factor complexes in ascus sets no. 114 and 157, for example (see table 5) was such that two non-dwarf and two dwarf component races received a full quota for optimum growth. The dwarfs, however could not respond because of the factor *v* for dwarfness which dominates but which cannot be dominant.

In figure 5 cultures of races 41.3 and 41.4 are not shown because they were exactly like races 41.1 and 41.2. This picture shows that race 41.1 produced very few ascocarps or perithecia. Each one matured many ascospores however. The cultures of race 41.2 produced great numbers of ascocarps. They were all completely sterile, that is, no asci ever developed. The picture of the non-dwarf component 41.2_1 shows many small incipient perithecia. Comparing component races 41.1_1 and 41.2_1 we see striking morphological differences although they are of the same mating type *a*. The dwarf components 41.1_2 and 41.2_2 are of the mating type *A*, but they differ in coloration and type of growth in culture. This all illustrates how there may be only two kinds of races derived from a single ascus if we consider only mating types and growth rates but four kinds considering mating types and morphological characters. Only when there has been a crossing-over at reduction in the ascus can there be, barring mutation, four kinds of progeny from the same ascus set.

In ascus set No. 44 a part of which is illustrated in figure 6 above, we see how two sets such as Nos. 41 and 44 can both be placed in the same Group, in this case Group II. B., yet represent entirely different types if we consider growth rates of their component races. Race 44.3 produces like race 41.1 only a few perithecia, each perithecium maturing many ascospores. Race 44.4 produces, like race 41.2, many sterile perithecia and no ascospores. They grew 10.3 and 10.9 cm. per day. The component races 44.3_1 and 44.4_1 grew only 5.5 cm. per day and look alike in culture. (Component races 41.1_1 and 41.2_1 were morphologically quite different.) Considering only morphological characters and mating types we have only two kinds of progeny, but when we add growth rates we have four kinds of progeny.

The average growth rate for forty-eight different f_1 haploid races of the type *AdV* was 2.4 cm. per day. The few possible errors in the determination of the factor *d* would not make a great difference in the average. Only two of these races, 154.1_{1b} and 154.2_{1b} grew noticeably faster. These two component races from ascus No. 154, a "Double" type, grew 6.6 cm. per day, which is nearly three times as fast as the original **C**$_4$ parent race, *AdV*, is growing now. Races 154.1_{1a} and 154.2_{1a} from this ascus and component mates of 154.1_{1b} and 154.2_{1b} respectively, grew 8.7 and 8.9 cm. per day respectively. These four non-dwarf races were retested several times with like results. Evidently a new combination of complementing growth factors had been effected. Parent race Dwarf **16** is *aDv*. Clearly *V* and *v* are not linked with *D*, *d* as we obtained forty-seven races which we recorded as *aDV* which showed an average growth rate of 9.42, twenty-one of which grew over 10 cm. per day. This indicates that each of these haploid *aDV* races could grow almost as fast as races **C**$_4$ and Dwarf **16** combined in heterocaryosis. Since each of these *aDV* races is homocaryotic and haploid, a redistribution of factors had occurred such that the suppressing (?) effects of the *v* factor carried originally by Dwarf **16** could no longer be possible because it had been replaced. Being of the normal or wild type of *N. tetrasperma*, *aDV*, we

would expect such races to grow much faster than either C_4 or C_8 both of which carry the growth "depressing" or "suppressing" lethal factor *d*, if we may express it this way.

There were thirty unisexual non-dwarf component races of the genotype *ADV*. A few of these were recorded rather doubtfully as to the factor *D*. Their average growth rate was 6.9 cm. per day, ranging from 1 cm. to 9 cm. per day as shown in the table. Races 136.3_{1a} and 136.4_{1b} were both *ADV*. They grew only 1.8 and 1.7 per day. No. 136.3 (= 136.3_{1a}) was a unisexual non-dwarf component of a Double non-dwarf. Its companion race 136.3_{1b} was not recovered. No. 136.4 was a Double non-dwarf. The component 136.4_{1a} *adV*, grew 7.6 cm. per day, and the component 136.4_{1b}, *ADV*, grew 1.7 cm. per day. The two components when reunited heterocaryotically grew 10.6 cm. per day, showing heterocaryotic vigor.

Our tester races, S_1 and S_9, *aDV* and *ADV*, respectively, when together in a heterocaryotic mycelium grow about 12 cm. per day. S_1 race grows by itself only about 7.8 cm. per day and race S_9 about 6 cm. per day. In race 136.4, a Double non-dwarf, we do not have "the depressing" effects, as just noted, of the dwarf *v* factor. Yet the individual growth rates of the components 136.4_{1a} and 136.4_{1b} are not up to that of the normal or wild types. There is still some factor carried by race 136.4_{1a} (*adV*) which complements some factor in 136.4_{1b} which is *ADV*. A comparable situation would be when race C_4, *AdV*, is grown with S_1, *aDV*. The average of some 169 24-hour tests for growth rate of C_4 was 2.17 cm. per day. While both C_4 and C_8 seem to grow much more slowly than they originally did, yet when now grown with Dwarf **16** the heterocaryotic mycelium grows over 12 cm. per day.

The average growth rate of twenty-nine races of the type *aDV* was 6.7 cm. per day, which was about the same as that of thirty races of the type *ADV*. For 122 tests of race C_8, which is *adV*, the average growth rate was 4.5 cm. per day. Whenever a Double non-dwarf f_1 race had its two components recorded as *ADV* and *adV*, or *AdV* and *aDV*, the heterocaryotic combination grew vigorously, i. e., from 10 to 12 cm. per day. This does not necessarily mean that every heterocaryotic race of the type *ADV–adV* or *AdV–aDV* would show heterocaryotic vigor. Four tests of f_1 heterocaryotic f_1 races from the cross $C_4 \times S_1$ (*AdV* × *aDV*) showed average growth rates of 7.2, 8.3, 7.3 and 6.8 respectively per day. One test of a heterocaryotic mixture 5.2_1-S_9, (*adV-ADV*), gave a rate of only 6.5 cm. per day. As these tests were of races heterocaryotic *d* and *D* we must believe that the tester race S_9, for example, no longer represents a typical rapidly growing wild type race although its genotype for the factors which we are considering is *ADV*. In other words the mere absence of nuclei carrying recessive lethal *d* in a *heterocaryotic* race such as given just above does not insure that that race will show heterocaryotic vigor.

In some experiments carried on earlier by the senior author through a series of back-crosses, a number of non-conidial races of the *tetrasperma* type were obtained. Some of them were proved to have the genotype *ADV* and others the genotype *aDV*. None of these produced conidia. Certain of these races of opposite mating types were recently grown together heterocaryotically. They showed very little evidence of heterocaryotic vigor although none of the nuclei in these bisexual races carried the recessive lethal *d*. We thus have some unisexual races which are non-conidial that grow slowly either by themselves or heterocaryotically with certain other non-conidial races of the opposite mating type.

In one test, our tester race S_1 averaged 7.8 cm. per day and race S_9 averaged 5.7 cm. Four f_1 races from the matings $S_1 + S_9$ averaged 12.2 cm. per day. Here we have a good example of complementing heterocaryotic vigor in which our factors *v* and *d* are not involved. Race Tex. 3, *ADV*, a wild type race of *N. tetrasperma* from Texas grew about 11.7 cm. per day. Tex. **6**, *aDV*, grew 12.4. The growth rate of Tex. **3** + Tex. **6** was about 12.3 cm. per day. We are indebted to Major C. G. Schmitt for wild type cultures of *N. tetrasperma* from Australia. Several unisexual races were isolated and their growth rates determined. It was found that they all grew 12 cm. or over per day. We made similar tests of races from the Canal Zone and from Puerto Rico with like results. There was little if any heterocaryotic vigor shown when races of opposite mating types were grown together. The two mating types could be readily distinguished by their color and type of growth in potato dextrose agar.

HETEROCARYOTIC VIGOR OF SECOND GENERATION f_2 RACES

Not much work has been done in determining growth rates of second generation races. A yel-

low f_1 dwarf originally numbered 130 was mated to C_4 and the four bisexual races from ascus No. 1 were studied. The components of each of the four heterocaryotic f_2 races were isolated. The results of these and many other tests prove that the complementing factor complexes are carried through Mendelian segregation to the f_2 races, and no doubt on through any number of generations. When it appeared that a heterocaryotic f_1 race was not showing vigor, f_2 races were obtained by germinating ascospores from the f_1 race. Tests of the f_2 races invariably showed heterocaryotic vigor, proving that the original f_1 race in question had not become evenly heterocaryotic.

GENETIC CONSIDERATIONS

This report does not attempt to include a formal genetic interpretation of our results as effects of certain definite gene complexes. It was interesting, however, to see how the eight component races, representing each of forty-six of those asci analyzed, were distributed, accepting as correct for purposes of this comment, their genotypes so far as was determined incidentally as a part of the routine. If a non-dwarf race like C_4 (*AdV*) is mated with dwarf 16 (*aDv*) there can be only eight types of homocaryotic f_1 progeny races, namely, *ADV*, *AdV*, *ADv*, *Adv* and *aDV*, *adV*, *aDv*, *adv*. However, when we distribute nuclei having these genotypes in groups of two among the four ascospores represented in different ascus types, we have, of course, a much larger combination number. One fact of importance seemed to be evident from our results. At no time did we obtain by germinating what appeared to be normal sized spores from an ascus, four f_1 races which were homocaryotic for mating types and yet heterocaryotic for other characters. For example ascus No. 112 seemed to have four normal sized f_1 spores, but the f_1 races were all found to be unisexual, sex *A*, mating type. Numerous attempts to separate out two different components from each of these four races always resulted in showing that each race was strictly homocaryotic for the characters with which we were concerned. The four nuclei that would carry the mating type factor *a* had been lost in some way, and along with them the genes which would, if present, have made the spore in each case heterocaryotic. It has been assumed heretofore that in the distribution of the eight nuclei, four of each sex, occasionally we would obtain four unisexual spores, but two of one mating type and two of the other. In each case there would be two like nuclei in each spore, at least alike as to their mating type. No doubt such a distribution does occasionally occur. Our forty sets of Doubles prove that two nuclei each carrying the factor either *V*, or *v* are often brought into the same spore. In all such cases one nucleus will carry *a* and the other *A*. Evidently the opposite mating type factors *A* and *a* tend to go together. In all our past experiences with *Neurospora tetrasperma* we have found only two ascospores that were heterocaryotic for mating types *A*, *a*, but homocaryotic, *d*, *d* for the recessive lethal.

The mating from which the f_1 races analyzed were obtained was $C_4 \times$ Dwarf **16** and therefore the parental genotypes or old combinations were *Ad* and *aD*. The eight components from each of 45 asci had been isolated and tested for mating types, *A* and *a* and also for *D* and *d*, the factors chiefly concerned with ascus abortion. Of the 360 races studied 200 tested as old combinations, *Ad* and *aD*, and 160 as new combinations, *AD* and *ad*, which is an indication of a linkage. However, our results as recorded did not show a single ascus from which we obtained four kinds of nuclei, namely *Ad*, *aD*, *AD*, and *ad*. This means that no simple crossing-over involving these factors had occurred. We cannot believe that all the new combinations had resulted from the chance distributions of chromosomes. Lindegren[11] reported that the + or sex gene of *N. Crassa* lies well out on the end of the sex chromosome. It is possible to cross this species with *N. tetrasperma*. This would indicate that in the latter species the genes for mating types would very likely be similarly located. However, as recorded, our results would have to be interpreted as showing that these genes are so near the centromeres that crossing-over at those points is very rare. Our present conclusions are that our tests for a few of the races were inadequate, and therefore crossing-over was not recognized. This phase of this question is being checked and will be reported on in the future. This would involve, first of all, the elimination of those incompatibility or sterility factors that would, if present, interfere with the growth of the perithecia, or would cause perithecium abortion by preventing the development of asci altogether. Asci homozygous, *dd*, eventually abort without forming spores, but asci that are heterozygous, *Dd*, delimit spores.

[11] Lindegren, C. C., The structure of the sex chromosome of *Neurospora crassa*, *Jour. Heredity* **27**: 251–259, 1936.

SUMMARY AND CONCLUSIONS

Asci of the so-called facultatively heterothallic species *Neurospora tetrasperma* contain normally four ascospores each of which develops two haploid nuclei which are of opposite mating types. The mycelia of the races derived from these spores will be heterocaryotic for the mating type factors *A*,*a* and they will grow about 12 cm. per day under our cultural conditions. It does not make much difference in the growth rates whether the wild type mycelia are homocaryotic or heterocaryotic. Our race **C**$_4$ has the genotype *AdV*. It differs from a unisexual homocaryotic wild type in that its nuclei carry a lethal *d* which not only affects the growth rate of the haploid mycelium but it also causes ascus abortion in an ascus whose diploid nucleus was homozygous *d*,*d* for this factor. The mycelial growth rate is now only about 2.5 cm. per day.

Our Yellow Dwarf **16** is a unisexual very slowly growing race. It has the genotype *aDv*. The factor *v* is the allele of *V* which means that this dwarf in two respects is like the wild type but is a dwarf because of the factor or deficiency, *v*, which has a very deleterious effect on growth rate in mycelia that are homocaryotic for *v*. Dwarf **16** grows only a fraction of a centimeter per day. When, however, races **C**$_4$ and Dwarf **16** are allowed to grow together in a mixed culture nuclear migrations occur which provide the cells of the mycelia with both kinds of nuclei, *AdV* and *aDv*, so they become heterocaryotic for all three pairs of factors. It has been found that such mycelia grow at the rate of from 10 to 12 cm. per day, about that of normal or wild type races. These new heterocaryotic races produce ascocarps abundantly and as the asci are heterozygous *Aa Dd Vv* they will delimit f_1 ascospores. In a rather large number of tests it has been found that these ascospores are usually heterocaryotic for mating type factors *A* and *a*, and for the factors *D* and *d*, the factor *D* may go with either factor *A* or factor *a*, and so with the factor *d*. The reason for this is not clear at present. On the other hand the f_1 ascospores are often homocaryotic for dwarf or for non-dwarf factors. Both nuclei in each of two of the four spores from an ascus will carry the wild type *V*, and the nuclei in the other two will both carry the factor for dwarfness or *v*. Such asci are called Doubles. Races from two of their four ascospores will be Double non-dwarfs, and from the other two Double dwarfs.

The results of our work prove, first, that when Dwarf **16** is united with race **C**$_4$ vegetatively so that the cells of the mycelium become heterocaryotic, the growth rate is greatly increased. We have called this effect heterocaryotic vigor. It is analogous to hybrid vigor in higher plants and animals. The work reported here proves beyond all doubt that the effects of genes located in different haploid nuclei, but in the same cytoplasm, are additive so that we may have a resultant effect of a number of gene forces acting together. In true hybrid vigor the complementing genes must be working together in each diploid nucleus, a single nucleus in each cell. In our haploid races of *Neurospora* each cell may have numerous haploid nuclei.

Race **C**$_4$ by itself is unable for some reason to synthesize all the necessary growth substances in sufficient quantities to insure a full wild type rate of growth. The same holds for race Yellow Dwarf **16**. When the two kinds of nuclei are brought together in the same cytoplasm to form a heterocaryotic structure there is a complementing effect which insures the synthesizing of a full quota of growth substances. The reason for this is not simple because we are dealing with two races which carry different lethal factors *d* and *v* respectively, both affecting growth rates. There appear also to be still other growth factors concerned since a similar complementing effect is found when races **S**$_1$ and **S**$_9$ are combined in a heterocaryotic mycelium. Neither of these races carries either lethal *d* which has of itself an effect to prevent a normal development, or the lethal *v* which has a strong dwarfing effect.

It has thus been proved that the factor complexes which determine heterocaryotic vigor such as described in this paper are heritable, being passed on in Mendelian segregation to f_1, f_2 generations and no doubt through any number of succeeding generations.

Races of *Neurospora tetrasperma*, heterocaryotic for mating types, originally from Texas, Puerto Rico, the Canal Zone and from Australia all grew about 12 cm. per day. In each case it was found that the unisexual components which are, of course, homocaryotic for mating types also grew vigorously or about 11 to 12 cm. per day. Growing the two components together again gave little evidence in any case of heterocaryotic vigor. No doubt a study of these races would result in the discovery of variants which would be unable to synthesize the necessary growth substances and which would respond to the complementing effects of other slowly growing races.

AN OUTLINE OF THE THEORY OF ATMOSPHERIC ECLIPSES

ZDENĚK KOPAL

Harvard College Observatory

ABSTRACT

The aim of the present paper will be to set up equations which relate the loss of light, during atmospheric eclipses, with the geometrical circumstances in close binary systems whose one (or both) component possesses an extended envelope. The presence of such an envelope around one (say the primary) component will, in general, cause its companion to suffer a gradual loss of light long before being eventually eclipsed by the photosphere of its mate. The respective loss of light should evidently depend on structural properties of the obscuring atmosphere as well as on the relative dimensions of both components and their positions in the orbit. Our ultimate aim will be to explore ways and means by which the properties of the atmosphere could be deduced from the changes of light exhibited during such an eclipse.

Following a general introduction (section I) we shall first investigate the optical depth of extended stellar atmospheres, characterized by spherical symmetry and constant extinction coefficient per unit mass, whose density decreases exponentially with height (section II). Under such circumstances the optical depth will be shown to be expressible rigorously in terms of modified Bessel functions of the second kind. In sections III and IV we shall proceed to evaluate the actual loss of light caused by the obscuring envelope during eclipses that are wholly or partly atmospheric. We shall find that, except for the special cases discussed in section IV, the loss of light itself is a rather difficult object for straightforward evaluation; but the rate of the changes of light during wholly atmospheric eclipses will prove to be obtainable with relative ease. In section IV we shall study to some detail shallow eclipses caused by atmospheres that are either very tenuous or very dense.

The concluding section V will be devoted to a discussion of the problem of determining the structural properties of an obscuring atmosphere from the changes of light observed during atmospheric eclipses. It is pointed out that the alternate minima exhibited by such binary systems are in general bound to be of unequal widths as well as peculiar form. An extended envelope surrounding the primary component will not only produce broad wings on the light curve at the time when the primary is in front, but will affect also the distribution of brightness over apparent disk of the primary star itself and so the form of the light curve in the alternate minimum as well. It is emphasized that only by a gradual harmonization of data pertaining to both minima genuine elements of such peculiar eclipsing systems may be obtained.

I. INTRODUCTION

IT is a matter of everday experience to verify that the limb of our Sun appears perfectly sharp, and physical reasons underlying this phenomenon have been well understood since the days of Schwarzschild.[1] The same reasons should apply also to all similar stars in general; and on the strength of this evidence it has long been assumed in the theory of light curves of eclipsing binary systems that their components, if actually seen, would appear in projection as sharp-edged disks. This assumption was based on sound physical considerations and led to satisfactory and coherent results in the vast majority of known eclipsing systems. The recent decade brought, however, the discovery of a number of binaries whose behavior in this respect may be expected to be anomalous: namely systems in which one (or both) components possess extended atmospheres. A classical example of one type of such variables is afforded by supergiant eclipsing systems ζ Aurigae or VV Cephei. In these and similar variables the early type component has near superior conjunction to pass behind extended atmosphere of its mate and suffer an appreciable loss of light before being eventually eclipsed by its photosphere. In other words, the bodily eclipses in these and similar systems are necessarily preceded by atmospheric eclipses of the early-type component, which may gradually merge one into another. A different type of atmospheric eclipses is represented by the Wolf-Rayet eclipsing binaries V 444 Cygni or the recently discovered HD 214419[2] where the dimensions of both components are probably of the same order of magnitude; and still another kind may be displayed by giant systems like RX or SX Cassiopeiae.[3] Since the systems showing evidence of atmospheric eclipses are likely to grow in numbers as well as importance at an accelerated pace, it seems desirable that a theory of atmospheric eclipses be developed along similar lines as that already existing for eclipse of opaque stellar disks. In the present paper an outline of such a theory will be given.

[1] Schwarzschild, K., *Nachr. K. Ges. Wiss. Göttingen*, No. 41, 1906.

[2] Gaposchkin, S., *Astrophys. Jour.* **100**: 242, 1944.

[3] Struve, O., *Astrophys. Jour.* **99**: 89, 1944. *Cf.* also Gaposchkin, S., *Astrophys. Jour.* **100**: 221 and 230, 1944.

In more specific terms, the object of any such theory must be to establish relations between observable quantities (i. e., the observed loss of light) and the absorbing power of the atmosphere as well as geometrical circumstances of the eclipse. In a general case, such a relation takes the form of an integral equation of the first kind with variable upper limit (Volterra's equation) a full-dressed solution of which appears wholly impracticable. It can be shown that if the component undergoing eclipse may be regarded as a luminous point (or, what is the same, if the occulting limb is regarded as a straight edge), Volterra's equation degenerates into one of the Abelian type which admits of a formal inversion.[4] When, however, the dimensions of both components are of the same order of magnitude Abel's theorem proves of no avail and some assumption relating the atmospheric density ρ and its extinction coefficient k with altitude h above the photosphere appears prerequisite. The present investigation is going to be based on the assumption that

$$\rho = \rho_0 e^{-ah}, \tag{1}$$

where ρ_0 and a are arbitrary constants, and that

$$k = \text{constant}. \tag{2}$$

The well-known equation (1) expresses the condition of hydrostatic equilibrium but its validity extends to more general cases—such as to atmospheres supported by the turbulence. There exists a sound observational evidence to show that turbulence is indeed responsible for the great extent of the atmosphere surrounding ζ Aurigae,[5] and the same may be true in many other systems as well. The condition (2) expressing the independence of the extinction coefficient on height is obvious whenever the atmospheric extinction is due to a scattering of light. If it were due partly or wholly to atomic absorption k should be expected to vary somewhat with height because of varying temperature. The temperature in extended stellar atmospheres is, however, known to vary very much less than the density; so that the condition (2) is likely to be fulfilled, rigorously or approximately, in most practical cases.

Once the relations (1) and (2) have been laid down the course of our investigation is specified. Our first step must be to determine the optical depth τ of the extended atmospheres along the line of sight and its variation with the phase. Then we may proceed to evaluate the actual loss of light, due to atmospheric extinction, by integrating the appropriate distribution of brightness over the disk of the eclipsed star. A mathematical analysis of these propositions will, unfortunately, prove to be anything but simple; and in order not to lose perspective of this outline in the midst of technical details recourse must be had to certain approximations. Thus throughout the present paper we shall assume that (1) the extended atmospheres are characterized by a spherical symmetry, and (2) the distortion of the component undergoing eclipse is likewise negligible and its disk, out of eclipses, would appear uniformly bright. In systems like ζ Aurigae as well as V 444 Cygni the latter is a harmless false assumption; for a distortion of the secondary components in these and similar systems is very small indeed and their early spectral types preclude any appreciable darkening at limb. On the other hand, in postulating spherical symmetry of extended atmospheres we find ourselves at once on a more objectionable ground; for the tidal action of the star undergoing eclipse is bound to distort this symmetry the more, the greater its mass. A partial justification of our above assumption other than its simplicity may, however, be derived from the fact that it should depart from reality most where the extinction is smallest—that is, in outer layers—whereas in inner and denser layers tides should be much less important.

Thus assuming a spherical symmetry of extended atmospheres and an exponential decrease of their density with altitude we shall find it possible to express their optical depth τ in a closed form as a function of the phase. The actual loss of light of a stellar disk of finite dimensions caused by a passage through an extended atmosphere will prove very difficult to evaluate—except when the eclipse is purely atmospheric[6] and so shallow that squares and higher powers of τ may be neglected. On the other hand, we shall find it much simpler to ascertain the rate of the variation of light with the phase regardless of the depth of the eclipse and irrespective of whether the eclipse is wholly or only partly atmospheric. This latter point

[4] The writer proposes to discuss this particular feature of the problem in a separate communication.

[5] *Cf.* Wellmann, *Veröff. Sternw. Berlin-Babelsberg* **12**, Heft 4, 1939.

[6] I.e., as long as the whole disk of the star undergoing eclipse could be seen, though dimly, through the atmosphere of its mate.

is important; for a distinction between wholly and partly atmospheric eclipses is geometrical rather than physical and will hereafter be made for convenience only. The extinction of inner layers of an extended atmosphere may occasionally prove so heavy that the star undergoing eclipse by it may effectively disappear before reaching the photosphere—i. e., may sink into obscurity like the sun setting in a smoky terrestrial atmosphere and disappearing before it reaches the horizon. A fuller discussion of the physical aspects of photospheres of stars possessing extended envelopes is wholly beyond the scope of this paper; the reader interested in this problem should consult the work of Kosirev[7] and Chandrasekhar.[8]

II. OPTICAL DEPTH OF AN OBSCURING ATMOSPHERE

Consider a star of photospheric radius R_1—which in what follows we shall consistently refer to as the primary component—surrounded by an extended atmosphere the density of which diminishes with altitude in accordance with (1) so that $\rho_0 = \rho(R_1)$ is the density at the base of the atmosphere. An envelope of this type should theoretically extend to infinity. For the purposes of this investigation the atmosphere may, however, be regarded as having effectively ended at distances at which its extinction becomes inappreciable. If this distance were larger than the orbital radius of the attending component, the companion should (apart from all other effects) be expected to display continuous variation of light in the course of the entire cycle that should simulate a reflection effect of the opposite sign. There exists, however, so far no evidence to show that extended atmosphere in any known eclipsing system would exert noticeable continuous absorption[9] at distances exceeding the separation of both components or even a sizeable fraction of it. Under such circumstances their existence should not affect the constancy of the combined light of a system over most part of the cycle to any appreciable degree, and their photometric effects should be confined to the neighborhood of conjunctions.

The optical depth τ of our atmosphere along the line of sight s is defined, as usual, by

$$d\tau = k\rho ds, \tag{3}$$

which within the scheme of approximation outlined in preceding paragraphs may be integrated into

$$\tau = 2k\rho_0 \int_0^\infty e^{-ah} ds. \tag{4}$$

On the other hand, h and s are geometrically related by

$$s^2 = (R_1 + h)^2 - (R_1 + h_0)^2, \tag{5}$$

where h_0 denotes the normal distance of the line of sight from the photosphere of the primary star. If we express the element ds from (4) in terms of dh by means of (5) and then change over to a new dimensionless variable x defined by

$$R_1 + h = x(R_1 + h_0),$$

our optical depth τ may be expressed as

$$\tau = b\alpha K_1(\alpha) \tag{6}$$

where

$$K_1(\alpha) = \int_1^\infty \frac{xe^{-\alpha x}}{\sqrt{x^2 - 1}}\, dx \tag{7}$$

and

$$\alpha = a(R_1 + h_0), \tag{8}$$

$$b = 2\frac{k\rho_0}{a} e^{aR_1}, \tag{9}$$

are constants which we shall later seek to determine.

As the reader may easily verify by application of any standard test, the integral (7) is convergent and defines a single-valued function of α. The explicit form of this function is indeed not hard to find. Integrating (7) by parts we find that

$$\int_1^\infty \frac{xe^{-\alpha x}}{\sqrt{x^2 - 1}}\, dx = \alpha \int_1^\infty e^{-\alpha x} \sqrt{x^2 - 1}\, dx, \tag{10}$$

and the latter integral can be identified as a member of a general family of functions defined by [10]

$$K_n(\alpha) = \frac{\sqrt{\pi}}{\Gamma(n + \frac{1}{2})} \left(\frac{\alpha}{2}\right)^n \int_1^\infty \frac{e^{-\alpha x} dx}{(x^2 - 1)^{\frac{1}{2} - n}}, \tag{11}$$

[7] *Monthly Notices Roy. Astron. Soc.* **94**: 430, 1934.

[8] *Ibid.* 444.

[9] A selective absorption extending beyond orbital radius of an eclipsing system has frequently been observed spectroscopically; but since such absorption is ordinarily limited to very few discrete wave lengths its variation will not influence the total light of the system to any appreciable degree.

[10] *Cf.*, for instance, Gray and Mathews, *A treatise on Bessel functions*, 50 (eq. 29), London, Macmillan, 1931.

which is known to satisfy the differential equation[11]

$$\frac{\partial^2 K_n}{\partial \alpha^2} + \frac{1}{\alpha}\frac{\partial K}{\partial \alpha} - \left(1 + \frac{n^2}{\alpha^2}\right) K_n = 0, \quad (12)$$

subject to the conditions that, for $n \neq 0$,

$$K_n(0) = \infty \quad \text{and} \quad K_n(\infty) = 0. \quad (13)$$

Equation (12) is easily recognized as Bessel's equation with purely imaginary argument, and its particular solution satisfying the conditions (13) is known as the modified Bessel function of the second kind. Our optical depth τ thus turns out proportional to the modified Bessel function of the second kind and of order one.

The actual construction of the respective solution of equation (12) is rather tedious and need not be reproduced here;[12] the result being that

$$K_1(\alpha) = \frac{1}{\alpha} + \left\{\gamma + \log\frac{\alpha}{2}\right\} \sum_{j=0}^{\infty} \frac{1}{j!(j+1)!} \times \left(\frac{\alpha}{2}\right)^{2j+1} - \sum_{j=1}^{\infty} \frac{1}{j!(j-1)!}\left(\frac{\alpha}{2}\right)^{2j-1} \times \left(1 + \frac{1}{2} + \frac{1}{3} \cdots + \frac{1}{j} - \frac{1}{2j}\right), \quad (14)$$

where $\gamma = 0.577215\cdots$ is Euler's well known constant. When $\alpha \to 0$,

$$\lim K_1(\alpha) = \lim \frac{1}{\alpha} = \infty, \quad (15.0)$$

while when $\alpha \to \infty$,

$$\lim K_1(\alpha) = \lim \sqrt{\frac{\pi}{2\alpha}}\, e^{-\alpha} = 0. \quad (15.1)$$

If α is small, the full-dressed form of our solution (14) may be closely approximated by

$$K_1(\alpha) \doteq \frac{1}{\alpha} + \frac{\alpha}{2}\log\frac{\alpha}{2}; \quad (16)$$

while if α is large, equation (12) is known to admit of an asymptotic solution[13]

$$K_1(\alpha) = \sqrt{\frac{\pi}{2\alpha}}\, e^{-\alpha}\left\{1 + \sum_{j=1}^{\infty} \frac{(4-1^2)(4-3^2)\cdots(4-[2j-1]^2)}{j!(8\alpha)^j}\right\}. \quad (17)$$

The expression on the right-hand side of this equation diverges if considered as an infinite series but can be made to represent (14) with an arbitrary precision provided that α is sufficiently large. In brief, while equation (16) may be regarded as an approximation to (14) sufficient for all astrophysical purposes provided that $\alpha \ll 1$, equation (17) should be used whenever there are reasons to expect that $\alpha \gg 1$. For $\alpha \sim 1$ equation (14) admits, unfortunately, of no essential simplification and would have to be used as it stands.

Equation (6) together with (8), (9), and (14) represents the general and rigorous answer to the object of our inquiry: namely an explicit expression for the optical depth τ of a spherically-symmetrical extended atmosphere whose properties are specified by (1) and (2). Our result should be of application to many extinction problems—such as those occurring in an analysis of light curves of many eclipsing systems as well as, for instance, in the interpretation of certain aspects of solar flash-spectra.[14] Attempts at an evaluation of the integral (7) have indeed been already made; but in the light of the preceding results it appears that all expressions for τ found thus far may be regarded as correct only in the limiting case when $\alpha \to \infty$ (i. e., to the zero-order term in the asymptotic expansion (17)[15]).

[11] A direct verification that the integral on the right-hand side of (11) satisfies this equation may be carried out as follows. Integrate and differentiate (11) with respect to α behind integral sign and then integrate by parts. This yields, together with (11), three separate equations containing two types of unknown integrals which may be eliminated. Differentiate the eliminant once more with respect to α; equation (12) (for $n = 1$) results.

[12] For the process of evaluation *cf.* any standard treatise on Bessel functions or, for example, Whittaker and Watson, *Modern Analysis*, chap. 17, Cambridge Univ. Press, 1920.

[13] It is interesting to note that the expression in curly brackets on the right-hand side of (17) can be represented by a confluent hypergeometric series of the form ${}_2F_0\left(\frac{3}{2}, -\frac{1}{2}; -\frac{1}{2\alpha}\right)$.

[14] Menzel, *Lick Publ.* **17**: 242, 1931.

[15] A development of an asymptotic expansion of (7) in inverse powers of α has previously been attempted by Menzel (*Harv. Circ.*, No. 417, 1936) in his work on the structure of the atmosphere of ζ Aurigae. It appears, however, that all terms, in his equation (7), of order higher than zero are in error, largely because of the fact that Menzel expanded the radical in the exponent of his equation (5) in a binomial series which converged only for $x < 1$, whereas the whole range of the independent variable was $0 \leqslant x \leqslant \infty$. Fortunately, this should in no way impair the value of Menzel's application to ζ Aurigae, since in actual computations all higher-order terms were discarded as small. Our above analysis has shown that the asymptotic series (17) does not converge so rapidly,

III. THEORETICAL LIGHT CURVES DURING ATMOSPHERIC ECLIPSES

Let us now come to investigate quantitatively the changes of light which will occur when, in the neighborhood of superior conjunction, the secondary component will project itself behind the atmosphere of its mate and thus undergo an atmospheric eclipse. Let $\mathfrak{L}$ denote the instantaneous luminosity of the secondary component and J, the true distribution of brightness over its apparent disk. A passage of its light through the extended atmosphere of its mate will cause the *apparent* distribution of brightness as seen by a distant observer *through* the atmosphere to be, not J, but $Je^{-\tau}$, where τ is the optical depth investigated in the preceding section. In consequence, if the secondary is regarded as a sphere with initially uniform distribution of brightness ($J = 1$), $\mathfrak{L}$ may evidently be expressed as

$$\mathfrak{L} = 2\int_{r_2}^{r_1} e^{-\tau} r \cos^{-1}\frac{r^2 + \delta^2 - R_2^2}{2\delta r}\, dr\,, \quad (18)$$

where R_2 stands for the radius of the secondary component; δ, for a separation of centers of both stars projected on the celestial sphere; and

$$\begin{aligned} r_1 &= \delta + R_2, \\ r_2 &= \delta - R_2 \text{ or } R_1, \end{aligned} \quad (19)$$

depending on whether the eclipse is wholly or only partly atmospheric. The independent variable r denotes evidently the distance of any point from the origin of coordinates which we shall identify with the projected center of gravity of the primary star.

Now in section II we found that $\tau = b\alpha K_1(\alpha)$ and $\alpha = a(R_1 + h_0) = ar$. The whole integrand in (18) is therefore a known function of r and the integration may in principle be carried out. Actually, however, this proves almost forbiddingly difficult without imposing rather severe restrictions on both b and α. On the other hand, a specification of the *rate* of variation of $\mathfrak{L}$ with the phase offers much less difficulty and may be effected as follows. Differentiating (18) with respect to δ we find after some reductions that

$$\frac{\partial \mathfrak{L}}{\partial \delta} = -2R_2\int_{\theta_0}^{\pi} e^{-\tau}\cos\theta\, d\theta, \quad (20)$$

where the new angular variable θ is related with r by means of

$$r^2 = R_2^2 + \delta^2 - 2\delta R_2\cos\theta, \quad (21)$$

and

$$\theta_0 = 0 \quad \text{or} \quad \cos^{-1}\frac{R_2^2 - R_1^2 + \delta^2}{2\delta R_2}, \quad (22)$$

depending on whether the eclipse is wholly or partly atmospheric.

In order to be able to integrate the right-hand side of (20) we have to express τ as a function of θ. This may be done by means of the addition theorem for modified Bessel functions, which states that[12]

$$\alpha K_1(\alpha) = \frac{2(R_2^2 + \delta^2 - 2\delta R_2\cos\theta)}{\delta R_2} \times \sum_{n=0}^{\infty}(n+1)C_n^1(\cos\theta)I_{n+1}(aR_2)K_{n+1}(a\delta) \quad (23)$$

where I and K denote the modified Bessel functions of the first[16] and second kind, respectively, and the C_n^1's are the Gegenbauer polynomials of order one.[17] The series on the right-hand side of (23) can be shown to converge absolutely when $\delta > R_2$, its n'th term being of the order of magnitude of $(R_2/\delta)^{n+1}$; if $\delta < R_2$, the convergence is restored by a mere interchange of arguments of the two Bessel functions. Equation (23) or its equivalent with reversed arguments represents therefore the optical depth of an extended atmosphere with any precision over the entire domain of practical interest, with the exception of a singular point at $\delta = R_2$.

As the reader has undoubtedly noticed, an appeal to the addition theorem expressed by equation (23) removed in one stroke the independent variable from arguments of the Bessel functions and confined it to the Gegenbauer polynomials which are rational algebraic func-

and the neglected terms are not as small, as it would have appeared on the face of Menzel's results; but even so an error committed by his neglect of all higher-order terms should certainly be smaller than the uncertainty of observational data on which Menzel's study was based.

[16] Modified Bessel functions of the first kind are particular solutions of equation (12) subject to the conditions that, for $n \neq 0$,

$$I_n(0) = 0 \quad \text{and} \quad I_n(\infty) = \infty. \quad (13.1)$$

Such functions of integral orders are defined by the series

$$I_n(\alpha) = \sum_{j=0}^{\infty}\frac{1}{j!(n+j)!}\left(\frac{\alpha}{2}\right)^{n+2j}. \quad (24)$$

[17] I.e., the coefficients of h in the expansion of $(1 - 2h\cos\theta + h^2)^{-1}$ in ascending powers of h. For a discussion of properties of the Gegenbauer polynomials *cf.*, for instance, Whittaker and Watson, *Modern Analysis*, §15.8.

tions of $\cos\theta$.[18] If we expand now the exponential behind the integral sign on the right-hand side of (20) in ascending powers of τ and make use of (25), the integral can be readily evaluated term-by-term. This method, while rigorous, may, however, require evaluation of too many terms and is therefore time-consuming; for unless τ is small the convergence of our exponential expansion may not be particularly rapid. In point of fact this way of approach appears inevitable only when the eclipse is only partly atmospheric and θ_0 differs from zero; while so long as it remains wholly of atmospheric origin ($\theta_0 = 0$) we may avail ourselves of the following elegant and highly successful approximation which consists in replacing the integral by a summation of a finite number of terms.

Equation (23) makes it evident that

$$e^{-\tau}\cos\theta = f(\cos\theta),$$

where $f(\cos\theta)$ stands for a homogeneous function of $\cos\theta$. Now it has been established by Bronwin[19] in a half-forgotten memoir almost a century ago that, provided $f(\cos\theta)$ is a function whose $2n$'th tabular differences are negligible,

$$\int_0^\pi f(\cos\theta)d\theta = \frac{\pi}{n}\sum_{j=1}^{n} f\left(\cos\frac{2j-1}{2n}\pi\right). \quad (25)$$

For instance, if $f(\cos\theta)$ were a polynomial of degree less than sixth,

$$\int_0^\pi e^{-\tau}\cos\theta d\theta = \frac{\pi}{2\sqrt{3}}\{e^{-\tau(\pi/6)} - e^{-\tau(5\pi/6)}\}; \quad (25.1)$$

if its degree were less than tenth,

$$\int_0^\pi e^{-\tau}\cos\theta d\theta = \frac{\pi}{5}\cos\left(\frac{\pi}{10}\right)\{e^{-\tau(\pi/10)} - e^{-\tau(9\pi/10)}\} + \frac{\pi}{5}\cos\left(\frac{3\pi}{10}\right)\{e^{-\tau(3\pi/10)} - e^{-\tau(7\pi/10)}\}; \quad (25.2)$$

and so on. An expansion of the exponential on the left-hand side of (20) and a comparison with (25) reveal that equation (25.1) or (25.2) is correct as far as terms of the order of $(R_2/\delta)^5$ or $(R_2/\delta)^9$ are concerned. In general, n terms of the right-hand side of (25) will approximate the integral on its left-hand side correctly to terms of the order of $(R_2/\delta)^{2n-1}$ or their reciprocals.

If, however, the eclipse happens to be only partly atmospheric ($\theta_0 \neq 0$), Bronwin's formula fails and recourse must be had to literal evaluation. Thus expanding the exponential on the right-hand side of (20) in ascending powers of τ we find that, to the first order in b,

$$\begin{aligned}\frac{\partial \mathfrak{L}}{\partial\delta} = &-4bR_2(\pi-\theta_0)\{x_1 - 2yx_2 + 6x_3 \\ &- 4yx_4 + \cdots\} - 4bR_2 y\sin\theta_0 \\ &\times\{x_1 + C_1^1 x_2 + (C_2^1 + 6)x_3 \\ &+ (C_3^1 + 4C_1^1)x_4 + \cdots\} \\ &- 4bR_2\sin\theta_0\{\tfrac{1}{2}C_1^1 x_1 + \tfrac{1}{3}(C_2^1 + 9)x_2 \\ &+ \tfrac{3}{8}(C_3^1 + 6C_1^1)x_3 + \tfrac{2}{5}(C_4^1 + 5C_2^1 \\ &\qquad + 20)x_4 + \cdots\},\end{aligned} \quad (26)$$

where

$$x_n = I_n(aR_2)K_n(a\delta) \quad \text{or} \quad I_n(a\delta)K_n(aR_2),$$

depending on whether $\delta \gtrless R_2$,

$$y = \frac{\delta^2 + R_2^2}{\delta R_2} \quad \text{and} \quad C_n^1 \equiv C_n^1(\cos\theta_0).$$

Equation (26) is exact as far as terms of the order of $(R_2/\delta)^4$ or its reciprocals are concerned. An extension to a higher order of accuracy may be carried out along exactly the same lines by anyone who may desire it.

It goes without saying that once the explicit form of (20) is known, $\mathfrak{L}$ may be obtained by quadratures. In practice this appears, however, to be not even necessary; for the observations furnish customarily $\mathfrak{L}$ as a function of δ,[20] and the rate of variation of $\mathfrak{L}$ with δ may therefore be deduced from the observed data by ordinary processes of numerical differentiation. With the left-hand side of equation (20) being regarded as known, our ultimate task should evidently consist of determining the constants a and b from known values of δ and R—or, for partial eclipses, of δ, R_1, and R_2. A mere glance at equations (18) or (20) should give us a sufficient warning that this will be by no means easy—in point of fact, the writer is thus far unable to indicate any specific method for obtaining such a solution other than the brutal procedure by trial and error. It appears therefore important to inquire whether or not equation (18) may not admit of a more direct solution than by way of (20) which, though not being general, may come

[18] The reader may notice that the Gegenbauer polynomials of order one and index n are equal to $\sin(n+1)\theta/\sin\theta$.

[19] *Philos. Mag.* **34**: 262, 1849.

[20] See equations (45) and (46), section V below.

close to reality under certain plausible conditions. As will be shown below, the answer is in the affirmative: namely provided that an eclipse is wholly atmospheric and so shallow that squares and higher powers of τ may be ignored, a direct solution of (18) takes indeed a practicable form if the argument α is either very large or very small. These two cases will be found to correspond to two distinct types of extended stellar atmospheres the former of which is likely to be of considerable astrophysical interest. The purpose of the next section will be to prove it.

IV. ASYMPTOTIC SOLUTIONS FOR SHALLOW ECLIPSES

Suppose that the exponential in the integrand of (18) is expanded in a series of the form

$$e^{-\tau} = 1 - \tau + \cdots.$$

This series is known to converge absolutely for $\tau < \infty$; but its first few terms are likely to give a fair representation of the exponential only if τ is small. The reader may remember that a layer of optical depth $\tau = 1$ will reduce the light passing through it to $1/e$'th of its original amount—which corresponds to a loss of approximately 1.086 magnitudes. We see, therefore, that as long as the depth of an atmospheric eclipse does not exceed one- or two-tenths of a magnitude τ may indeed be regarded as small enough for its squares and higher powers to be neglected.

Within this scheme of approximation a direct solution of (18) may be approached as follows. Let

$$\mathfrak{L} = \mathfrak{L}_0(1 - \Delta\mathfrak{L}), \tag{27}$$

where $\mathfrak{L}_0 = \pi R_2^2$ stands for full light of the secondary component and $\Delta\mathfrak{L}$ denotes the fractional loss of light at any moment during atmospheric eclipse. Then, as long as the eclipse remains wholly atmospheric,

$$\pi R_2^2 \Delta\mathfrak{L} = 2b\int_{r_2}^{r_1} \alpha K_1(\alpha) r \cos^{-1}\frac{\delta^2 - R_2^2 + r^2}{2\delta r}\,dr, \tag{28}$$

where $r_2 = \delta - R_2$. Since the use of a rigorous expression for $K_1(\alpha)$ as given by equation (14) would still lead to rather intractable analysis, we propose in what follows to limit ourselves to the evaluation of the foregoing integral in the cases when $K_1(\alpha)$ may be satisfactorily approximated by equations (16) or (17). The former approximation was found to hold good when α is so small that $\alpha K_1(\alpha)$ is close to unity; the latter, when α is large and consequently $\alpha K(\alpha)$ goes to zero. Now α can be generally small only if a is small; and if τ is to remain small it follows that b—or, more exactly, the ratio ρ_0/a—must then be small. This demonstrates that α and τ can be small simultaneously only if the respective atmosphere is tenuous. On the other hand, if α and consequently a is large, the smallness of τ is automatically ensured by virtue of (15.1)—in fact if α is large, so must be ρ_0 in order that the eclipse shall not become negligible. In brief, the approximation (16) should in reality be applicable to *tenuous* atmospheres characterized by *low* density-gradient, whereas equation (17) should correspond to *thick* atmospheres whose density-gradient is *steep*.

Let us begin by considering the former alternative first. Combining (7) and (16) we find that the optical depth of a tenuous atmosphere should sensibly vary as[21]

$$\tau = b\left(1 + \frac{\alpha^2}{2}\log\frac{\alpha}{2}\right), \tag{29}$$

and the corresponding loss of light $\Delta\mathfrak{L}$ during shallow eclipse of a uniformly bright star may be expressed as

$$\Delta\mathfrak{L} = b\left\{1 + \frac{a^2 I}{\pi R_2^2}\right\}, \tag{30}$$

where

$$I = \int_{r_2}^{r_1} r^2 \log\frac{ar}{2}\cos^{-1}\frac{r^2 + \delta^2 - R_2^2}{2\delta r}\,dr. \tag{31}$$

This latter integral may be solved wholly in terms of the elementary functions. Its actual evaluation is, however, much too long to be reproduced here in full—though the result will prove to be fairly simple. After repeated partial integration and several changes of the independent variable we ultimately establish that

$$I = \frac{\pi R_2^4}{4}\left\{1 + \left(1 + 2\frac{\delta^2}{R_2^2}\right)\log\frac{a\delta}{2}\right\}, \tag{32}$$

and the fractional loss of light then takes the concise form

$$\Delta\mathfrak{L} = b + \tfrac{1}{4}a^2 b R_2^2 \times \{1 + (1 + 2\cot^4\lambda)\log(aR_2\cot\lambda)\}, \tag{33}$$

[21] The reader may notice that when $\alpha \to 0$ and, consequently, $K_1(\alpha) \to 1/\alpha$ the optical depth of the respective atmosphere remains sensibly constant and independent of the phase. The light of the secondary as seen through such an atmosphere would merely be reduced to $e^{-b}\mathfrak{L}_0$ In order for this actually to happen it would, however, be necessary for α to be as small as 0.01 or less.

where

$$2\lambda = \sin^{-1} k = \cos^{-1} (r_2/r_1) \qquad (33.1)$$

is a function of the phase.

The second alternative corresponding to thick atmospheres, characterized by steep density-gradient, will lead to more intricate mathematics. In this case the optical depth of the respective atmosphere can be approximated by

$$\tau = b\sqrt{\frac{\pi\alpha}{2}}\, e^{-\alpha}\, {}_2F_0\left(\frac{3}{2}, -\frac{1}{2}; -\frac{1}{2\alpha}\right), \qquad (34)$$

and the corresponding loss of light during shallow eclipses then turns out expressible in terms of integrals of the form

$$\int_{r_2}^{r_1} r^j \sqrt{r} e^{-ar} \cos^{-1} \frac{r^2 + \delta^2 - R_2^2}{2\delta r}\, dr \equiv J_j(a), \qquad j \geqslant 1. \qquad (35)$$

These integrals are again convergent for any positive value of a and we may notice that

$$\frac{\partial J_j}{\partial a} + J_{j+1} = 0. \qquad (36)$$

In order to evaluate them, substitute $r = x^2$ on the left-hand side of (35) and integrate by parts. If we differentiate then the resulting relation with respect to a and make use of (36) we find that the $J_j(a)$'s are bound to satisfy the following linear differential equation

$$\frac{\partial}{\partial a}(aJ_j) + (j + \tfrac{1}{2})J_j = Q_j \qquad (37)$$

of the first order, where

$$Q_j(a) = 2\int_{\sqrt{r_2}}^{\sqrt{r_1}} \frac{x^{2(j+1)}(x^4 - r_1 r_2)e^{-ax^2}}{\sqrt{(r_1^2 - x^4)(x^4 - r_2^2)}}\, dx. \qquad (38)$$

The solution of (37) which remains finite for $a = 0$ is known to be

$$J_j(a) = a^{-(j+\frac{1}{2})} \int a^{j+\frac{1}{2}} Q_j(a)\, da. \qquad (39)$$

It does not seem possible to advance the evaluation of J in a closed form beyond this point; for even when $a = 0$, Q_j remains an integral of the hyperelliptic type. In what follows we shall, therefore, seek an asymptotic expression for J valid when the relative dimensions of the component undergoing eclipse are small.

In order to do so, substitute

$$x^4 = r_1^2(1 - k^2 y^2)$$

where the modulus k is defined by (33.1), and expand (39) in terms of ascending powers of k^2; we find that

$$J_j(a) = \frac{\pi}{32} r_1^{j+\frac{1}{2}} k^4 e^{-ar_1} \times \left\{1 + \frac{1}{8}(5 + 2ar_1 - 2j)k^2 + \cdots\right\}. \qquad (40)$$

Collecting all previous formulae we ultimately establish that

$$\Delta\mathfrak{L} = ab(\delta + R_2)\cos^4\lambda \times \{K_1(ar_1) + \tfrac{1}{4}ar_1 K_2(ar_1)k^2 + \cdots\}, \qquad (41)$$

where, as before, $2\lambda = \sin^{-1} k$.

In the case of thick atmospheres characterized by steep density-gradient the fractional loss of light during a shallow eclipse thus turns out expansible in terms of modified Bessel functions of the second kind. The resulting series is again asymptotic—i. e., it diverges if regarded as an infinite series, but can be made to approximate the actual loss of light with any accuracy provided that k^2 is sufficiently small. Now in reality k can be small if R_2 is small in comparison with δ; and this in turn implies that the first few terms on the right-hand side of (41) should provide a sufficient approximation to reality only when the relative dimensions of the component undergoing eclipse are small. The solution for $\Delta\mathfrak{L}$ we were able to obtain in the case of a thick obscuring atmosphere is therefore decidedly less general than that for tenuous atmospheres; for the latter was exact for any value of k.

The reader may also verify that, when $R_2 \to 0$, both equations (33) and (41) reduce to $\Delta\mathfrak{L} = \tau$ exactly as they ought to; for as long as the star undergoing eclipse may be regarded as a luminous point we have, rigorously,

$$\Delta\mathfrak{L} = 1 - e^{-\tau}, \qquad (42)$$

which for small values of τ reduces to the result.

V. APPLICATION TO PRACTICAL CASES

In preceding sections our aim has been to establish formulae which relate the loss of light, during atmospheric eclipses, with geometrical circumstances of the respective eclipse as well as structural properties of the obscuring atmosphere. We found the actual relationship between these quantities to be quite complex; and were able to deduce its explicit form only under certain restricting conditions. The form of the

light curve of an atmospheric eclipse was found to be peculiar, characterized by broad wings, and quite different from any theoretical light curve corresponding to eclipses of two opaque stellar disks; formulae derived in sections III and IV put us in a position to predict the form of an atmospheric eclipse when properties of the obscuring atmosphere are given. The latter are, however, but seldom known *a priori*. On the contrary, the problem which may often confront us in practice is exactly the reverse and may be briefly stated as follows: *given the geometrical circumstances, deduce the properties of an obscuring atmosphere from the changes of light observed during atmospheric eclipse*. In more specific terms, since throughout the present investigation we have presumed the structure of this atmosphere to be governed by (1) and (2), our aim should be to determine values of the constants a and $k\rho_0$—or a and b—from quantities that are observable or can be considered as otherwise known.

In full generality, the problem at issue proves to be so complicated as to make it advisable for us to approach it in steps. First, let us consider the limiting case when $R_2 \to 0$—i. e., when the component undergoing eclipse may be regarded as a luminous point. Equation (42) is then exact and, on taking logarithms, we find that, in this case,

$$\log (1 - \Delta \mathfrak{V}) = \tau = 2\delta k\rho_0 e^{aR_1} K_1(a\delta). \quad (43)$$

If, moreover, $a\delta$ is so large that

$$K_1(ar_1) \to \sqrt{\frac{\pi}{2ar_1}}\, e^{-ar_1},$$

equation (43) may further be reduced to

$$\log \frac{\log (1 - \Delta \mathfrak{V})}{\sqrt{2\pi\delta}} = \log \frac{k\rho_0}{\sqrt{a}} - (\delta - R_1)a. \quad (44)$$

The left-hand side of this equation as well as the coefficient $(\delta - R_1)$ being known from observations, (44) may be regarded as a linear equation for determining the unknown values of a and of $\log (k\rho_0/\sqrt{a})$. As many equations of the form (44) can be set up as there are normal points observed within an atmospheric eclipse; and their least-squares solution should yield the most probable values of the unknowns.

It may be briefly mentioned at this stage how the values of $\Delta \mathfrak{V}$ and δ are actually deduced from the observations. If, as usual, the luminosity of the whole eclipsing system between minima is taken as the unit of light and l denotes the system's actual light observed at any particular phase, then

$$\Delta \mathfrak{V} = \frac{1 - l}{L_2}, \quad (45)$$

where L_2 stands for the fractional luminosity of the component undergoing atmospheric eclipse (i. e., a normalized value of $\mathfrak{V}_0$). It is also a matter of simple geometry to prove that the apparent separation of centers of the components projected on the celestial sphere is given by

$$\delta^2 = R^2(1 - \sin^2 i \cos^2 \psi), \quad (46)$$

where R denotes the actual instantaneous separation of the components in their relative orbit; ψ, the secondary's true anomaly (phase-angle) reckoned from the moment of conjunction; and i, the inclination of the orbital plane to the celestial sphere. The reader should notice that equations (45) and (46) contain two quantities that are directly observable (l, ψ) and two others (L_2, i) that can be inferred only through the medium of an intermediary orbit deduced from an analysis of the light changes during the alternate eclipse (see later).

The above-described procedure pivoting around the equation (43) should be ample for dealing with atmospheric eclipses in systems like ζ Aurigae or VV Cephei, where the dimensions of the early-type component are indeed very small in comparison with those of the red supergiant. When, however, the component undergoing atmospheric eclipse can no longer be regarded as a luminous point (V 444 Cygni), a determination of structural properties of the obscuring atmosphere becomes more difficult. Letting, for brevity's sake,

$$b = x, \qquad \delta/R_2 = \cot^2 \lambda,$$
$$aR_2 = y, \quad a(\delta + R_2) = y \csc^2 \lambda = \eta,$$

where x and y are dimensionless quantities and λ is the same function of phase as defined by equation (33.1), we may bring equations (33) and (41) to the common form

$$\frac{\Delta \mathfrak{V}(\lambda)}{f(\lambda, y)} = x, \quad (47)$$

where, for tenuous atmospheres ($\eta \ll 1$),

$$f(\lambda, y) = 1 + \frac{y^2}{4} \times \{1 + (1 + 2\cot^2\lambda)\log(y\cot\lambda)\}; \quad (48.0)$$

while for thick atmospheres ($\eta \gg 1$),

$$f(\lambda, y) = \cos^2\lambda\cot^2\lambda \times \{yK_1(\eta) + y^2\cos^2\lambda K_2(\eta) + \cdots\}. \quad (48.1)$$

It is to be remembered that both foregoing equations (48) hold good for shallow eclipses only. The latter converges, moreover, only provided that y is small and this, coupled with the condition that $\eta \gg 1$, requires that λ be small (i. e., $\delta \gg R_2$). Thus, unlike (48.0), equation (48.1) will approximate a theoretical light curve only at early stages of the respective atmospheric eclipse. It is easy to see, however, that this limitation is precisely equivalent to the neglect, in equation (28), of all powers of τ higher than the first: namely an atmospheric eclipse cannot remain shallow at advanced phases if the obscuring atmosphere is thick; while for tenuous atmospheres the eclipse may remain shallow throughout.

It does not appear possible to solve equations (47)–(48) for x and y in any other way than by trial and error. Given a set of $\Delta\mathfrak{L}$'s observed at different stages of the eclipse, we must search, by trial and error, for such a value of y that will render the left-hand side of equation (47) constant. In other words, we should seek to determine y as such a quantity that will reduce equation (47), plotted in the $\Delta\mathfrak{L} - f$-coordinates, to a straight line. The slope of such a line would then indicate x. Once both x and y have been determined, the final unknowns may be found from

$$a = \frac{y}{R_2} \quad \text{and} \quad k\rho_0 = \frac{xy}{2R_2}\, e^{-y(R_1/R_2)}. \quad (49)$$

A specification of x and y from the observed data by means of equation (47) should not require any undue amount of labor. In the case of tenuous atmospheres all functions constituting $f(\lambda, y)$ are elementary; for thick atmospheres the computation of $f(\lambda, y)$ may be greatly facilitated by the use of existing tables of the K-functions.[22]

[22] For a very complete and up-to-date bibliography of such tables *cf.* Bateman and Archibald, A guide to tables of Bessel functions, *Jour. Math. Tables and other aids to computation* **1**: 205, 1944.

It should not be forgotten, however, that equations (47) and (48) are directly applicable to reality only when the eclipses are shallow, purely atmospheric, and the obscuring envelope is very tenuous or very thick. Should any of these conditions break down, recourse must be had to the full-dressed formulae derived in section III; that is, the derivatives $\partial\mathfrak{L}/\partial\delta$ must be computed and x, y eventually solved for—in the absence of any more equitable alternative—again by trial and error.

In conclusion, it should be noted that a determination of structural properties of an obscuring atmosphere from the changes of light observed during atmospheric eclipse requires, in general, a knowledge of the geometrical elements of the respective eclipsing system and, in addition, that of the radius of the star undergoing eclipse in absolute units. That is, apart from quantities directly observed (l, ψ), L_2 and $\cos i$ are needed to specify x and y; whereas a knowledge of the absolute value of R_2 as well as that of the ratio of R_1/R_2 is prerequisite for the ultimate determination of a and $k\rho_0$.

Such being the situation, the idea suggests itself to deduce the elements of our system solely from an analysis of its light curve in the minimum due to an eclipse of the star possessing an extended envelope. If this latter eclipse were total or annular the task should be simple enough; if it were partial the situation may become difficult. But whatever may be the case, we should keep well in mind that the distribution of brightness over apparent disk of the primary star, and therefore the elements we are going to obtain, depend also on the properties of the extended envelope which are unknown at this early stage of orbital analysis. In order to obtain the elements we have once more resorted to successive approximations. We know, on general grounds, that an extended envelope is likely to exaggerate the darkening at limb of the star which is imbedded in it.[7,8] Let us therefore determine first the geometrical elements of our system from an analysis of its light curve during eclipse of the primary component assuming the latter to be completely darkened at limb. With the aid of elements thus obtained analyze the light changes due the atmospheric eclipse of the secondary component half a revolution later and determine a and $k\rho_0$. Then deduce the actual distribution of brightness on the primary's apparent disk appropriate to the

values of a and $k\rho_0$ just found[23] and see whether or not this new distribution of brightness will cause any significant change in the geometrical elements arrived at previously. If so, repeat the whole procedure with improved elements and continue so long until all elements are stabilized.

[23] For the respective formulae *cf.* Chandrasekhar, S., *op. cit.*

There are good reasons to expect that such approximations should as a rule be rapidly convergent; but even if they were not they could hardly be avoided. Fot it is only through a gradual harmonization of the complete observational evidence pertaining to both minima that we may gain some insight into the structure of such superlatively intriguing phenomena as close binaries possessing extended atmospheres.

THE NUMBERS OF VERTEBRAE IN PRIMATES

ADOLPH H. SCHULTZ AND WILLIAM L. STRAUS, JR.

Department of Anatomy, Johns Hopkins University

INTRODUCTION

THE numbers of vertebrae in the different regions of the spinal column can change with evolution and can vary individually to a considerable extent. It is a reasonable assumption that evolutionary changes in the modal number of vertebrae in a particular spinal region are the result of definite hereditary trends for the occurrence of individual variations in the number of vertebrae forming that region. Any comparative study of the numbers of segments in the various regions of the vertebral column in different groups of animals must deal with the closely connected problems of variability and of evolutionary specialization.

The present paper concerns itself with the numbers of vertebrae in the mammalian order Primates. That these numbers have undergone change with evolution in primates has already been demonstrated by Rosenberg (1876), Keith (1903), Todd (1922), Gadow (1933), and others, though on the basis of rather limited material. This publication is intended, first of all, as a record of new and uniformly gathered observations on extensive series of specimens; but it also forms a contribution to the study of the phylogenetic relationships between the various types of primates, with special regard to man, and adds to our knowledge of the degrees of variability in different primates and in the different regions of the spine. Inasmuch as this report deals exclusively with the numerical variations of vertebrae, it demonstrates the regional differentiation in the spinal column only in so far as the number of affected segments is concerned. It does not take into consideration the many other manifestations of gradual regional transition occurring in the form of variations in such features as the number of ribs reaching the sternum, the relative lengths of the last ribs, the position of the lumbo-sacral border in relation to the ilia, the number of sacral vertebrae articulating with the ilia, and of the so-called pseudo-sacral vertebrae, etc.

The literature contains a great deal of information concerning the numbers of vertebrae in primates, and from the many, though widely scattered, available sources one could collect very considerable series of data. Unfortunately, however, there still exists no universal agreement regarding the precise definition of the different types of vertebrae. This lack of uniformity in the literature concerning the characters which determine the regional allocation of a vertebra is clearly shown by the following few examples, selected at random: Flower (1885), in his classic work on the osteology of mammals, states that the sacrum of the great apes is generally composed of five vertebrae "to which the last lumbar not unfrequently becomes united in old animals. The whole sacrum thus formed is long and narrow. . . ." This implies that a lumbar vertebra can change into a sacral one late in life and that the vertebral formulae of young and of old animals are not comparable. Such a conclusion can no longer be maintained. In his monumental study on vertebral variations, Le Double (1912) deals with cases of "fifth lumbar" vertebrae, unilaterally or even bilaterally sacralized, in the section devoted to the lumbar region and does not count such vertebrae as sacral ones. In a report on skeletons of American Indians, Hrdlička (1916) gives a photograph of a sacrum, containing six segments, but lacking fusion between the first two vertebrae (plate 26, *a*). This is entitled "Sacrum showing bilateral articulation with an extra segment introduced between the last lumbar and the sacrum." Apparently this "extra" vertebra has not been assigned to either the lumbar or the sacral region and hence the statistical data in this report cannot be compared with corresponding data by other authors. Fick (1933, 1936), who has published observations on the vertebrae of many anthropoid apes, determines the number of sacral segments by a somewhat arbitrary and peculiar method which certainly does not depend upon the number of sacral foramina. Many authors have failed to define the criteria they employed in interpreting transitional vertebral forms and frequently no reference at all is made to vertebrae having the character of one region on one side and that of the ad-

joining region on the opposite side; yet, from the size of the series examined, such asymmetrical vertebrae would be expected. For these reasons it is evident that, unfortunately, the records contained in the literature are not, or may not be, strictly comparable. The writers have been reluctantly forced to the conclusion that it is safest to disregard all relevant data in the literature for the present statistical purposes, though reference occasionally will be made in the text to data collected by other authors. By limiting this report to the writers' own observations, at least in so far as all tabulations are concerned, it still will be possible to deal with the subject matter on the basis of more records than have been available to previous authors, except in regard to man. A total of 1457 primate skeletons has been examined for the vertebral formulae by the writers of this paper. This material includes the great majority of the extant primate genera and permits a comprehensive survey of the entire order. To supply certain data, which could not be obtained by the writers from their own observations, and for the purpose of comparison, reference occasionally will be made in the text or in footnotes to the vertebral formulae of certain primate skeletons in the Hamann Museum of Western Reserve University. These particular data, hitherto unpublished, were collected by Mr. Arthur W. Todd and are used here with the generous permission of the late Professor T. Wingate Todd (letter of January 5, 1934). These formulae are not always strictly comparable with those of the writers, inasmuch as in the former there is no recognition of transitional vertebrae as such. Asymmetrical vertebrae, apparently, had been completely relegated to either of the two regions involved. On account of this difference, the data of Mr. Todd could not be included in the tables, but they are mentioned wherever helpful and are always ascribed to A. W. Todd.

The following definitions applicable to primates have been strictly adhered to by the writers in their examination of specimens:

1. CERVICAL VERTEBRAE = the vertebrae between the skull and the thorax. An atlas, fused with the occiput, or one with incomplete formation of the dorsal or ventral arch, is counted as ***one*** vertebra. In cases with so-called cervical ribs the vertebra bearing these structures is counted as a cervical if the costal parts are incomplete and possess free ventral ends; but as a thoracic if the ribs reach the sternum directly, or indirectly by way of the adjacent ribs. Consistently, an eighth vertebra without ribs or with only incomplete ribs, ending freely, is regarded as a cervical segment. These interpretations do not follow the usage prevailing in the anatomical and medical literature, but correspond to the customary definitions of variations at the caudal end of the thoracic region of the spinal column and agree with the comparative-anatomical practice of stating the number of cervical vertebrae as, e. g., 6 in one type of sloth (*Choloepus*) and as 9 in another (*Bradypus*), simply and correctly because complete ribs are present on the seventh segment in the former and begin at the tenth segment in the latter. All instances with a fully formed rib on one side and the lack of such a rib on the opposite side of a vertebra at the border between the cervical and thoracic regions are regarded as transitional, cervico-thoracic vertebrae and are counted as half a cervical vertebra and half a thoracic one.
2. THORACIC VERTEBRAE = the vertebrae bearing ribs. At the caudal end of this region the last pair of ribs may be represented by mere rudiments which furthermore may be ankylosed and immovable. Even such cases are included among the thoracic vertebrae. The occurrence of a rib on one side and of a true transverse process only on the opposite side characterizes the segment as a transitional or thoraco-lumbar vertebra[1] which is counted as half a thoracic and half a lumbar vertebra.
3. LUMBAR VERTEBRAE = the vertebrae between the thorax and the sacrum, bearing no ribs or possessing no lateral masses participating in the formation of sacral foramina. It is specially mentioned that if the transverse processes of a vertebra articulate even extensively with the ilia, but do not form sacral foramina together with the following vertebra, the former segment is regarded as a lumbar one. If the transverse and costal elements of a vertebra meet (with or without fusion) the corresponding parts of the adjoining vertebra lateral to an intervertebral foramen, thus forming a

[1] The term "thoraco-lumbar" will be applied here only to asymmetrical, transitional vertebrae to conform with the corresponding, restricted use of the terms cervico-thoracic, lumbo-sacral and sacro-caudal. The combined series of all thoracic and lumbar vertebrae, commonly referred to as "thoraco-lumbar" vertebrae, will be designated *thoracic + lumbar* vertebrae to avoid confusion.

continuous articulation with the ilium, the vertebra is counted as a sacral whenever these conditions exist bilaterally, and as a lumbo-sacral, if unilaterally.

4. SACRAL VERTEBRAE = the vertebrae composing the sacrum and possessing intervertebral and sacral foramina ringed completely by bone in the adult. Actual osseous fusion is not necessary, but contact between the sacral wing portions of adjoining vertebrae, lateral to the sacral foramina, must exist in either a bony or cartilaginous state. The number of sacral vertebrae equals half the number of sacral foramina plus one. The number of sacral foramina, however, at times can differ on the two sides in consequence of asymmetrical formations at either end of the sacral region. Such transitional lumbo-sacral or sacro-caudal vertebrae are classified by half segments (see fig. 2).
5. CAUDAL OR COCCYGEAL VERTEBRAE = all remaining vertebrae, following upon the sacral ones. Since the latter already have been defined there is no need for further specifications. It merely remains to be mentioned that the terminal segments of the caudal region are often of minute size and may have become lost, *post mortem* or, at times, even by *intra vitam* amputation. Among the higher primates the last two or more coccygeal vertebrae occasionally are fused in such a manner that the total number of coccygeal elements cannot be determined with certainty. In all doubtful cases the highest possible number has been recorded, this followed by a question mark. Naturally, records with question marks are omitted in the calculation of averages and in ranges of variations. In rare instances the last coccygeal segment can be represented by two separate bony elements, lying side by side, or may be forked. This is regarded as a single, though abnormal, vertebra. Half a caudal or coccygeal vertebra always refers to the existence of a sacro-caudal, respectively sacro-coccygeal, vertebra.

It will be noted that in the tables to follow the totals of the specimens examined sometimes are smaller than the corresponding totals in table 1. This is owing to the fact that some of the available spinal columns were incomplete for a variety of reasons. Most frequently it was the caudal region which lacked some segments, this because the small terminal vertebrae had become lost or had been left in the skin.

In a comparative study, such as this, which deals with material representing an entire mammalian order, the taxonomic nomenclature employed and the systematic grouping of the specimens studied must be briefly explained. This is particularly necessary in the case of the primates, which have been classified by different authors in widely different manners. Indeed, there exists as yet but little agreement even regarding the names of many genera and families. Figure 1 gives the list and classification of recent primates which has been tentatively adopted by the writers on the basis of their own knowledge of primates and also as representing a compromise between the many different schemes proposed by students of primate morphology, particularly those dealing with significant anatomical rather than strictly taxonomic characters, as e. g. Gregory (1916, 1920), Weber (1927–1928), Simpson (1931), Abel (1931), and Clark (1934). The generic and other names selected for this tabulation are those most commonly used in the literature of the last three decades and do not necessarily consider the intricate problems of priority. The terms "Simiae" and "Pongidae" have been chosen deliberately in place of the frequently used names "Anthropoidea," and "Anthropomorpha," in order to avoid all possible misunderstandings arising from the use of the well-established term "anthropoids." The name "Simiae" for the third suborder recommends itself also because this group is composed of all true simian primates and because all other primates belonging to the first and second sub-orders frequently are referred to as "prosimiae." The anthropoids have here been placed in a single family, consisting of two subfamilies, as has been done also by Gregory (1916), Sonntag (1924) and others. This emphasizes the present view of the writers that the gibbons and the great apes form one natural family and are separated from each other by differences of at most subfamily rank. It also must be mentioned here that some taxonomists recognize more genera of recent primates than are given in figure 1. Elliot (1913), e g., lists 2 genera of Galaginae (*Galago* and *Hemigalago*), 3 genera of tamarins (*Leontocebus*, *Seniocebus* and "*Cercopithecus*") and 3 genera of macaques (*Pithecus*, *Magus*, *Simia*). Pocock (1926) distinguishes between 2 genera of baboons (*Papio* and *Mandrillus*) and lists 6 different genera in the subfamily of Semno-

SUBORDER		FAMILY	SUBFAMILY	GENUS	ENGLISH NAME
LEMUROIDEA		DAUBENTONIIDAE		DAUBENTONIA	Aye-Aye
		LEMURIDAE	LEMURINAE	LEMUR	True Lemur
				MYOXICEBUS	Gentle Lemur
				LEPIDOLEMUR	Sportive Lemur
				MIXOCEBUS	Hattock
			CHIROGALEINAE	ALTILILEMUR	Fat-tail Lemur
				MICROCEBUS	Dwarf Lemur
				CHIROGALE	Mouse Lemur
			INDRISINAE	INDRIS	Indris
				LICHANOTUS	Avahi
				PROPITHECUS	Sifaka
		LORISIDAE	LORISINAE	LORIS	Slender Loris
				NYCTICEBUS	Slow Loris
				ARCTOCEBUS	Angwantibo
				PERODICTICUS	Potto
			GALAGINAE	GALAGO	Bush Baby
TARSIOIDEA		TARSIIDAE		TARSIUS	Tarsier
SIMIAE	SERIES PLATYRRHINAE	HAPALIDAE		HAPALE	True Marmoset
				OEDIPOMIDAS	Marmoset
				LEONTOCEBUS	Tamarin
		CEBIDAE	CALLIMICONINAE	CALLIMICO	Callimico
			AOTINAE	CALLICEBUS	Titi Monkey
				AOTUS	Night Monkey
			PITHECINAE	PITHECIA	Saki
				CACAJAO	Uakari
			ALOUATTINAE	ALOUATTA	Howler Monkey
			CEBINAE	SAIMIRI	Squirrel Monkey
				CEBUS	Capuchin Monkey
			ATELINAE	LAGOTHRIX	Woolly Monkey
				ATELES	Spider Monkey
				BRACHYTELES	Woolly Spider Monkey
	SERIES CATARRHINAE	CERCOPITHECIDAE	CERCOPITHECINAE	MACACA	Macaque
				CYNOPITHECUS	Black Ape
				PAPIO	Baboon
				THEROPITHECUS	Gelada
				CERCOCEBUS	Mangabey
				CERCOPITHECUS	Guenon
				ERYTHROCEBUS	Red Guenon
			SEMNOPITHECINAE	SEMNOPITHECUS	Langur
				RHINOPITHECUS	Snub-nose Langur
				NASALIS	Proboscis Monkey
				COLOBUS	Guereza
		PONGIDAE	HYLOBATINAE	HYLOBATES	Gibbon
				SYMPHALANGUS	Siamang
			PONGINAE	PONGO	Orang-utan
				PAN	Chimpanzee
				GORILLA	Gorilla
		HOMINIDAE		HOMO	Man

FIG. 1. The classification of the recent genera of primates, representing a compromise between the various versions proposed by different authors and considering especially anatomical characters revealing genetic relationships.

pithecinae, by splitting particularly the langurs into several generic groups. Allen (1925) has placed the hamadryas baboon in a separate genus (*Comopithecus*) and other taxonomists have proposed the creation of additional new genera; while a few of the genera contained in figure 1 have not been universally accepted. Miller (1933), e. g., does not recognize the genus *Symphalangus*, but places the siamangs in the genus *Hylobates*, which he divides into 4 subgenera. The writers are here concerned with the morphological classification of primates, indicating genetic relationships, rather than with purely taxonomic groupings, often based upon differences selected merely as being consistently applicable, but not necessarily morphologically significant.[2] Figure 1, therefore, represents an attempt to limit the generic subdivisions of primates to groups of approximately equal morphological value for use as a base in this comparative study. It is specifically stated here that in this paper all tamarins are included in the genus *Leontocebus*, the Celebes macaques and the Barbary ape have been assigned to the genus *Macaca*, the hamadryas, the drill and the mandrill, together with all other baboons, constitute the one genus *Papio*, all langurs are placed in the single genus *Semnopithecus*, and the so-called pygmy siamang (formerly *Symphalangus klossi*, renamed *Hylobates klossi*) is included with the gibbons in the genus *Hylobates*, in accordance with the findings of Schultz (1932, 1933). Other and rare forms, such as the guenon-like talapoin and the mangabey-like Hamlyn's monkey, require no discussion here since no specimens have been available for examination.

MATERIAL

Table 1 shows the distribution of the 1457 primate skeletons examined according to genera and to collections. The genera are listed in the same sequence as in figure 1, but do not include the following seven rare forms which were not available for this study: *Mixocebus*, *Altililemur*, *Indris*, *Propithecus*, *Arctocebus*, *Callimico*, and *Rhinopithecus*. The 41 genera which could be investigated represent all subfamilies with the exception of the Callimiconinae. The size of the generic series varies widely and in many instances the present data are based on only a few individual records which may not be typical for the genus. The best representation was obtainable among the catarrhine primates, particularly the anthropoids. Different generic series are theoretically not always comparable since they are composed of widely different numbers of taxonomic species. For instance, the genera *Nasalis* and *Homo* each contain only one species, whereas in the genus *Cercopithecus*, Pocock (1907) recognizes 42 species and Elliot (1913) 68, while additional species have been described since these revisions appeared. As will be shown in a later chapter, the inclusion of different species does not, as a rule, increase the total range of variations in a genus above the range within single species of the same genus, if the generic series are good-sized. Flagrant exceptions to this rule, however, can occur, as for instance in regard to the numbers of tail vertebrae in macaques. For this reason the findings in series of single species will be dealt with separately only if this is needed and possible. To record the present data according to species would have increased the size of the tables enormously without significant gains. For most of the genera studies two or more species have been available. It is specially mentioned here that the series of *Oedipomidas* is composed entirely of specimens belonging to the species *O. geoffroyi* from the Panama Canal Zone and that the great majority of the gibbons are of the species *Hylobates lar*. The series of *Homo* contains mostly negroes, but also whites and a few representatives of still other races.

The columns for *Collections* in table 1 are arranged according to the totals of specimens from each collection. The largest amount of material from one collection is that of the Museum of Comparative Zoology at Harvard comprising particularly the specimens collected by the Asiatic Primate Expedition of 1937. This, as much as of the other material, already has served in several previous reports by the senior author (Schultz, 1938, 1940, 1941, 1942, 1944). These publications contain information on this material which need not be repeated here. Further data on other material used here can be found in several other papers (Schultz, 1930, 1933, 1934). The writers are greatly indebted to the authorities in charge of the collections, listed in table 1, for their generous permission to examine all these primate skeletons.

[2] For instance, to place the hamadryas baboon in a genus of its own merely on account of the mantle of long hair in fully grown males, as has been done by Allen (1925), may be a useful procedure in pure taxonomy and justifiable for the sake of convenience in classifying; but it tends to be harmful, rather than helpful, in the investigation of comparative anatomical and phylogenetic problems.

TABLE 1

NUMBERS OF PRIMATE SKELETONS EXAMINED IN DIFFERENT COLLECTIONS

Collection / Genus	M. Z.	J. H.	N. M.	A. S.	A. M.	W. R.	S. W.	C. S.	U. M.	C. M.	U. Z.	W. I.	P. M.	P. A.	Y. U.	R. M.	M. C.	C. E.	M. P.	Total
Daubentonia	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2
Lemur	—	—	4	—	14	1	—	4	—	—	—	—	—	—	—	—	—	—	—	23
Myoxicebus	—	—	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Lepidolemur	—	—	1	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3
Microcebus	—	—	3	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	5
Chirogale	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Lichanotus	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
Loris	—	—	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Nycticebus	1	—	1	1	4	1	—	—	—	—	—	—	—	—	—	—	—	—	—	8
Perodicticus	—	3	5	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11
Galago	—	—	9	—	5	1	—	3	—	—	—	—	—	—	—	—	—	—	—	18
Tarsius	—	1	2	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Hapale	—	—	2	—	6	—	—	2	—	—	—	—	—	—	—	—	—	—	—	10
Oedipomidas	—	—	—	56	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	57
Leontocebus	—	—	3	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Callicebus	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Aotus	—	—	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7
Pithecia	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Cacajao	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Alouatta	—	4	7	5	3	—	—	—	—	—	2	—	—	—	—	—	—	—	—	21
Saimiri	—	—	—	4	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	5
Cebus	—	11	3	6	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25
Lagothrix	—	—	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Ateles	—	4	4	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16
Brachyteles	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1

TABLE 1—*Continued*

Collection / Genus	M. Z.	J. H.	N. M.	A. S.	A. M.	W. R.	S. W.	C. S.	U. M.	C. M.	U. Z.	W. I.	P. M.	P. A.	Y. U.	R. M.	M. C.	C. E.	M. P.	Total
Macaca	30	103	16	28	11	—	—	4	—	—	—	—	—	—	—	—	—	3	—	197
Cynopithecus	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Papio	—	17	14	2	17	—	—	—	—	—	2	—	—	—	—	—	—	—	—	52
Theropithecus	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
Cercocebus	—	9	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12
Cercopithecus	—	10	18	4	5	—	—	1	—	—	—	—	—	—	—	—	—	—	—	38
Erythrocebus	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Semnopithecus	78	1	27	7	3	—	—	3	—	—	—	—	—	—	—	—	—	—	—	119
Nasalis	39	—	6	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	49
Colobus	—	—	1	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6
Hylobates	154	2	29	63	10	1	38	—	—	11	3	—	5	—	—	—	1	—	—	318
Symphalangus	—	—	7	2	2	2	—	1	—	—	1	—	—	—	—	1	—	—	—	17
Pongo	13	1	44	19	7	2	—	5	—	1	4	11	1	3	—	4	2	—	1	121
Pan	2	42	18	18	3	2	—	—	—	—	2	—	—	—	5	—	—	—	1	93
Gorilla	12	13	12	2	7	3	—	—	—	5	1	1	—	3	1	—	—	—	—	61
Homo	—	62	—	1	—	32	—	—	23	—	—	—	—	—	—	—	—	—	—	118
Total:	329	283	263	238	125	47	38	28	23	17	15	12	6	6	6	5	3	3	2	1457

The following specimens are included in the totals, but are not tabulated according to collection: 1 gorilla in Musée du Congo Belge, Bruxelles, 1 orang-utan in Jefferson Medical College, 1 in Army Medical Museum, Washington, and 1 in Museum of Kuching, Sarawak, 1 siamang in Natural History Museum of Bern, Switzerland, 1 gibbon in Anatomy Department of Columbia University, 1 macaque in Anatomy Department of University of Wisconsin and 1 in possession of Mr. C. F. Stein, Jr. Key to Abbreviations: M. Z. = Museum of Compar. Zoology, Harvard University; J. H. = Anatomy Department, Johns Hopkins University; N. M. = U. S. National Museum; A. S. = collection of A. H. Schultz; A. M. = American Museum of Natural History; W. R. = Anatomy Department, Western Reserve University; S. W. = collection of S. L. Washburn; C. S. = Royal College of Surgeons, London; U. M. = Anatomy Department, University of Maryland; C. M. = Chicago Natural History Museum; U. Z. = collections of University of Zurich, Switzerland; W. I. = Wistar Institute of Anatomy; P. M. = Peabody Museum, Harvard University; P. A. = Philadelphia Academy of Natural Sciences; Y. U. = material from Yale University; R. M. = Raffles Museum, Singapore; M. C. = Medical College of Singapore; C. E. = Embryology Department, Carnegie Institution; M. P. = Musée d'Anatomie Comparée, Paris.

To future students of vertebral formulae in primates, table 1 serves to show for which genera additional information is most needed. The table also will be helpful in avoiding duplication of data by indicating which collections have already, and which others have not yet been utilized for the purposes of this study.

SPINAL REGIONS

CERVICAL VERTEBRAE

The number of cervical vertebrae in primates equals 7 with few individual exceptions. Seven cervical vertebrae are the rule in living and fossil mammals from which only sporadic and specialized forms have departed. Since no evolutionary change has affected the number of cervical segments in any of the primates, the cervico-thoracic border is characterized by remarkable stability not only intergenerically, but also intraspecifically.[3] A reduction in the number of cervical vertebrae to 6 occurs in the following specimens, examined by the writers: 1 macaque, 3 gibbons, 2 orang-utans, and 1 man. Six and a half cervical vertebrae were found in 1 macaque, 1 orang-utan, and 1 gorilla. Eight cervical vertebrae, finally, were observed in 1 gibbon. Deviations from the modal number of 7 cervical vertebrae occur in the present material with the following percentage frequencies: Macaque = 1.1, gibbon = 1.3, orang-utan = 2.5, gorilla = 1.6, and man = 0.9; in all other primate genera the corresponding figure is 0. Such deviations have thus far been encountered in all of the higher primates save the chimpanzee. A. W. Todd, like the writers, found no instance in his series of (70) chimpanzees. That numerical variations in cervical vertebrae are very rare in primates is shown also by the fact that the literature apparently contains only three papers by other authors recording such cases in non-human primates: 8 cervical vertebrae have been found in a siamang by Kohlbrügge (1891) and in a gorilla by Struthers (1893), and 6 cervical vertebrae have been recorded by Nayak (1933) for a *Perodicticus potto*. A. W. Todd found 8 cervicals in one of 6 specimens of *Indris indris* and 6 cervicals in a *Lemur variegatus*. A considerable number of human skeletons with 6 cervical vertebrae and a few with 8 have been described, but previous information regarding the percentage frequency of such variations in man seems not to have existed. According to Le Double (1912), complete or incomplete ribs on the seventh vertebra occurred in 2.2 per cent of (902) human skeletons, but in all probability most of these cases possessed merely cervical ribs and not a reduced number of cervical vertebrae in the sense of the present definition.

[3] In calculating the numbers of precaudal and of all vertebrae it appeared justifiable to assume that the number of cervical segments is 7 in those few specimens for which—for various reasons—exact data on this region had been unobtainable.

THORACIC VERTEBRAE

The number of the thoracic vertebrae, in striking contrast to the number of cervical ones, varies very extensively among mammals in general and primates in particular. Since, as mentioned above, the cervico-thoracic border is comparatively stable, it obviously must be the thoraco-lumbar border which is readily shifted, thus accounting for the marked fluctuations in the number of segments forming the thoracic region of the spine. Thirteen thoracic vertebrae may be presumed to represent the primitive, ancestral number for primates (see also Keith, 1903). In the tree shrews, which among all living mammals probably have changed least from the common ancestor of all primates, there are 13 thoracic vertebrae. At least, this is the condition in 11 specimens of *Tupaia* and in one of *Tana* examined by the writers, as well as in one *Tupaia* of the National Museum studied by Lyon (1913), which had not been available to the writers. The number of thoracic segments also was 13 in a specimen of another tree shrew, *Dendrogale*, studied by Davis (1938). In the pen-tailed tree shrew, *Ptilocercus*, however, there are 14 thoracic vertebrae in the specimens recorded by Jentink (1885), Gregory (1913), and Clark (1926).

Among the recent primates the number of thoracic vertebrae varies individually between only 11 and as much as 18, as shown by the data in table 2. The modal numbers of the genera range between 12 and 16. On the assumption that the primitive thoracic spine contained 13 vertebrae, it may be concluded that among the primates there have occurred phylogenetic trends to increase as well as to decrease this number. In the two prosimian suborders, 12 or 13 thoracic vertebrae are the rule, excepting only the subfamily Lorisinae which is characterized by a very pronounced tendency for higher numbers of these vertebrae; indeed, 16 or more thoracic vertebrae are found exclusively in this subfamily of primates. The number of thoracic vertebrae in

TABLE 2

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF THORACIC VERTEBRAE AND AVERAGE NUMBERS OF THESE VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Number of Thoracic Vertebrae								Average
		11	12	13	14	15	16	17	18	
Daubentonia	2	—	**50**	50 —	—	—	—	—	—	12.3
Lemur	22	—	**86**	14	—	—	—	—	—	12.1
Myoxicebus	4	25	**75**	—	—	—	—	—	—	11.8
Lepidolemur	3	—	**100**	—	—	—	—	—	—	12.0
Microcebus	5	—	—	**80**	20	—	—	—	—	13.2
Chirogale	2	—	—	**100**	—	—	—	—	—	13.0
Lichanotus	3	—	**100**	—	—	—	—	—	—	12.0
Loris	6	—	—	17	—	**83**	—	—	—	14.7
Nycticebus	8	—	—	—	12	13	**38**	25	12	16.1
Perodicticus	11	—	—	—	27	18	**46** 9	—	—	15.3
Galago	18	—	—	**78**	22	—	—	—	—	13.2
Tarsius	7	—	14	**86**	—	—	—	—	—	12.9
Hapale	9	—	33	**67**	—	—	—	—	—	12.7
Oedipomidas	57	—	61	2 37	—	—	—	—	—	12.4
Leontocebus	4	—	**100**	—	—	—	—	—	—	12.0
Callicebus	2	—	**100**	—	—	—	—	—	—	12.0
Aotus	7	—	—	—	14 **86**	—	—	—	—	13.9
Pithecia	2	—	50	**50**	—	—	—	—	—	12.5
Cacajao	1	—	—	**100**	—	—	—	—	—	13.0
Alouatta	21	—	—	10	**71**	19	—	—	—	14.1
Saimiri	5	—	—	**60** 20	20	—	—	—	—	13.3
Cebus	24	—	—	13	**79**	8	—	—	—	14.0
Lagothrix	6	—	—	17	**83**	—	—	—	—	13.8
Ateles	16	—	—	—	**94**	6	—	—	—	14.1
Brachyteles	1	—	—	**100**	—	—	—	—	—	13.0
Macaca	196	—	**83**	3 14	—	—	—	—	—	12.2
Cynopithecus	4	—	**100**	—	—	—	—	—	—	12.0
Papio	52	—	**52**	6 42	—	—	—	—	—	12.5
Theropithecus	2	—	**50**	50	—	—	—	—	—	12.5
Cercocebus	12	—	**67**	8 25	—	—	—	—	—	12.3
Cercopithecus	38	— 2	**79**	3 16	—	—	—	—	—	12.2
Erythrocebus	1	—	**100**	—	—	—	—	—	—	12.0
Semnopithecus	119	1	**98**	1 1	—	—	—	—	—	12.0
Nasalis	49	—	**92**	8	—	—	—	—	—	12.1
Colobus	6	—	**100**	—	—	—	—	—	—	12.0
Hylobates	318	—	3	1 **83** 1	12	—	—	—	—	13.1
Symphalangus	17	—	18	**82**	—	—	—	—	—	12.8
Pongo	121	14 6	**75**	1 4	—	—	—	—	—	11.9
Pan	93	—	1	**80** 3	16	—	—	—	—	13.2
Gorilla	58	—	10	3 **81** 2	4	—	—	—	—	12.9
Homo	110	4 1	**94**	1	—	—	—	—	—	12.0

The most frequent variation, representing the modal number of vertebrae in a given genus, is shown in heavy type. In this and the following, similar tables the figures half-way between the columns for the numbers of vertebrae shown on top indicate the occurrence of specimens possessing asymmetrical transition vertebrae. For instance, in the genus *Homo* there are 11½ thoracic vertebrae in 1 per cent of the cases.

the suborder Simiae varies between 12 and 15 in the platyrrhine series, whereas between 11 and 14 in the catarrhine series. The Old World family Cercopithecidae has a modal number of 12 in all its genera. A decrease to only 11 thoracic vertebrae, never observed in New World monkeys, was found by the writers in only 1 specimen among all the Cercopithecidae examined. On the other hand, the number of 13 thoracic vertebrae persists in 62 of the Cercopithecidae listed in table 2. According to the data of A. W. Todd, only 11 thoracic vertebrae occurred but once among New World monkeys (namely, in one of two specimens of *Oedipomidas oedipus*) and twice among Old World monkeys (of which one case belongs to the genus *Cercocebus* and the other, as the instance of the writers, to the genus *Semnopithecus*). Fifteen thoracic vertebrae, never found by the writers in any catarrhine primate, have been recorded by A. W. Todd for a specimen of *Hylobates agilis*.

Among the higher primates (= families Pongidae and Hominidae) the modal number for thoracic vertebrae equals 13 in gibbon, siamang, chimpanzee,[4] and gorilla,[5] but only 12 in orang-utan and man. It is only in the latter two types of simian primates that the extreme reduction to 11 thoracic segments occurs with significant frequency. It is interesting to note that phylogenetic changes from the assumed primitive condition of 13 thoracic vertebrae have shifted the modal number by but one segment in either direction in the great majority of all primate genera and that the ranges of individual variations in each of these genera never extend over more than 3 segments, with the modal number occurring in at least 50 per cent of the specimens. The striking exception to this rule is found in *Nycticebus*, the genus with the highest average number of thoracic vertebrae. In this form the modal number of segments has become increased by 3, but exists in only 38 per cent of the specimens, and the range of individual variations extends over 5 vertebrae.

In the order Primates the first thoracic segment is the eighth vertebra of the spinal column with extremely few exceptions, but the last thoracic segment can be represented by any vertebra between the eighteenth and the twenty-fifth. This remarkable stability of the cephalic border and great instability of the caudal border of the thoracic region also is evident from the following comparison: Asymmetrical, or half, thoracic vertebrae exist in the present material at the cervico-thoracic border in only 3 specimens, whereas at the thoraco-lumbar border in 37 specimens.

LUMBAR VERTEBRAE

Among the tree shrews the number of lumbar vertebrae equals 6 in one specimen of *Tana* and in 10 out of 11 specimens of *Tupaia* examined by

[4] The series of 69 chimpanzees recorded by A. W. Todd has an average number of 13.0 thoracic vertebrae (range = 12 to 14) and the modal number of 13 exists in 93 per cent.

[5] In his large series of 171 gorillas, Randall (1944) found an average of 13.0 thoracic vertebrae (range = 12 to 14), with the modal number 13 occurring in 83.6 per cent.

TABLE 3

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF LUMBAR VERTEBRAE AND AVERAGE NUMBERS OF THESE VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Number of Lumbar Vertebrae								Average
		3	4	5	6	7	8	9	10	
Daubentonia	2	—	—	—	—	50 **50**	—	—	—	6.8
Lemur	22	—	—	—	27	**73**	—	—	—	6.7
Myoxicebus	4	—	—	—	—	**75**	25	—	—	7.3
Lepidolemur	3	—	—	—	—	—	—	**67**	33	9.3
Microcebus	5	—	—	—	40	**60**	—	—	—	6.6
Chirogale	2	—	—	—	—	**100**	—	—	—	7.0
Lichanotus	3	—	—	—	—	—	**100**	—	—	8.0
Loris	6	—	—	—	—	—	**67**	33	—	8.3
Nycticebus	8	—	—	12	—	12 **38**	38	—	—	7.1
Perodicticus	11	—	9	9	**46**	27	9	—	—	6.2
Galago	18	—	—	6	**83**	5 6	—	—	—	6.0
Tarsius	7	—	—	—	**86**	14	—	—	—	6.1
Hapale	9	—	—	—	**67**	33	—	—	—	6.3
Oedipomidas	57	—	—	—	35	4 **61**	—	—	—	6.6
Leontocebus	4	—	—	—	—	**100**	—	—	—	7.0
Callicebus	2	—	—	—	—	**50**	50	—	—	7.5
Aotus	7	—	—	—	—	**86**	14 —	—	—	7.1
Pithecia	2	—	—	—	**50**	50	—	—	—	6.5
Cacajao	1	—	—	—	**100**	—	—	—	—	6.0
Alouatta	21	—	—	**86**	14	—	—	—	—	5.1
Saimiri	5	—	—	—	20	20 **60**	—	—	—	6.7
Cebus	24	—	4	25	4 **67**	—	—	—	—	5.6
Lagothrix	6	—	**67**	33	—	—	—	—	—	4.3
Ateles	16	—	**94**	6	—	—	—	—	—	4.1
Brachyteles	1	—	—	**100**	—	—	—	—	—	5.0
Macaca	196	—	—	—	13	4 **81**	1	1	—	6.9
Cynopithecus	4	—	—	—	25	**75**	—	—	—	6.8
Papio	52	—	—	—	46	6 **48**	—	—	—	6.5
Theropithecus	2	—	—	—	50	**50**	—	—	—	6.5
Cercocebus	12	—	—	—	42	8 **50**	—	—	—	6.5
Cercopithecus	37	—	—	—	13	3 **81**	3 —	—	—	6.9
Erythrocebus	1	—	—	—	—	**100**	—	—	—	7.0
Semnopithecus	119	—	—	—	6	2 **91**	1	1	—	7.0
Nasalis	49	—	—	—	10	**90**	—	—	—	6.9
Colobus	6	—	—	—	17	**83**	—	—	—	6.8
Hylobates	318	—	5	1 **76**	3 15	—	—	—	—	5.1
Symphalangus	17	—	47	**53**	—	—	—	—	—	4.5
Pongo	120	7	6 **76**	1 10	—	—	—	—	—	4.0
Pan	93	38	6 **56**	—	—	—	—	—	—	3.6
Gorilla	58	29	5 **66**	—	—	—	—	—	—	3.7
Homo	109	—	5	1 **90**	4	—	—	—	—	5.0

the writers. The remaining *Tupaia* has only 5 of these vertebrae. Lyon (1913) gives 6 lumbar segments for another *Tupaia* in the National Museum which has not been seen by the writers. *Dendrogale* also possesses 6 lumbar segments according to the report by Davis (1938), whereas *Ptilocercus* has only 5, as recorded by Jentink (1885), Gregory (1913), and Clark (1926). Six lumbar vertebrae presumably represent the original condition in primates. A modal number of 6 lumbars has been retained by *Tarsius*, *Galago*, and *Perodicticus* among the prosimians and by a few platyrrhine genera, as shown by table 3. This mode has increased to 7, 8, or even 9 in a majority of the lemuroid genera. In many New World and in all Old World monkeys the modal number is 7. Fewer than the presumed original 6 lumbar vertebrae occur, on an average, in the platyrrhine subfamilies Alouattinae and Atelinae, and in all higher primates. In the Atelinae, the siamang and the three great apes, occurrences of 6 lumbar vertebrae have disappeared even as individual variations. The great apes, or Ponginae, are the only primates showing the extreme individual reductions to only 3 lumbar vertebrae. According to the literature, this reduction occasionally can be even greater. For instance, Fick (1933) has listed two gorillas with only 1½ lumbar vertebrae, though of one of these cases he was not certain inasmuch as the skeleton was incomplete. Randall's (1944) report on gorillas contains a case with 2 lumbar vertebrae.[6] The opposite extreme, consisting of an increase to 10 lumbar vertebrae, has been found by the writers in only one genus, i. e., *Lepidolemur*. According to the data of A. W. Todd, 10 lumbar vertebrae exist also in one of 6 specimens of *Indris indris* and are combined with 8 cervical, 11 thoracic, and 3 sacral segments. Four of these specimens have 9 lumbar and 12 thoracic vertebrae, whereas the remaining specimen has 8 and 13, respectively. The highest average number of lumbar vertebrae (9.3) occurs in the genus *Lepidolemur* and the lowest (3.6) in the genus *Pan*.[7] Man, with an average of 5 lumbar vertebrae, has undergone a smaller phylogenetic change than have many other primates.

Transitional, or half, lumbar vertebrae occur more frequently at the cephalic than at the caudal end of the lumbar region, indicating that the lumbo-sacral border is more stable than the thoraco-lumbar border. In the present material, such half vertebrae have been found 37 times at the latter border, whereas only 25 times at the former border.

SACRAL VERTEBRAE

It is highly probable that the original number of sacral vertebrae in ancestral forms of primates was 3. In 9 out of 10 specimens of *Tupaia* and in one of *Tana*, examined for this study, the sacrum is composed of 3 segments and in only one *Tupaia* does it contain 4 vertebrae. Three sacral vertebrae exist also in another *Tupaia*, listed by Lyon (1913), and in the other tree shrews *Dendrogale* (Davis, 1938) and *Ptilocercus* (Jentink, 1885; Clark, 1926). In the order Primates the number of sacral vertebrae is anywhere

[6] Randall (1944) obtained an average of 3.7 lumbar vertebrae in 175 gorillas (range = 2 to 4) and found the modal number of 4 in 68 per cent.

[7] In the series of 71 chimpanzees, studied by A. W. Todd, the number of lumbar vertebrae averages 3.8 (range = 3 to 5) and the modal number of 4 is present in 77 per cent.

TABLE 4

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF SACRAL VERTEBRAE AND AVERAGE NUMBERS OF THESE VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Number of Sacral Vertebrae							Average
		2	3	4	5	6	7	8	
Daubentonia	2	—	100	—	—	—	—	—	3.0
Lemur	21	9.5	86	—	—	—	—	—	2.9
Myoxicebus	4	—	100	—	—	—	—	—	3.0
Lepidolemur	3	—	67	—	33	—	—	—	3.7
Microcebus	5	20	80	—	—	—	—	—	2.8
Chirogale	1	—	100	—	—	—	—	—	3.0
Lichanotus	3	—	34.33	33	—	—	—	—	3.5
Loris	4	—	25	—	75	—	—	—	4.5
Nycticebus	6	—	—	—	17	50.16	17	—	6.1
Perodicticus	11	—	—	9	9	46	9.18	9	6.1
Galago	17	18.6	76	—	—	—	—	—	2.8
Tarsius	6	—	100	—	—	—	—	—	3.0
Hapale	9	22	78	—	—	—	—	—	2.8
Oedipomidas	57	— 2	98	—	—	—	—	—	3.0
Leontocebus	3	33	67	—	—	—	—	—	2.7
Callicebus	2	—	100	—	—	—	—	—	3.0
Aotus	6	—	100	—	—	—	—	—	3.0
Pithecia	2	—	100	—	—	—	—	—	3.0
Cacajao	1	—	—	100	—	—	—	—	4.0
Alouatta	20	—	80	20	—	—	—	—	3.2
Saimiri	5	—	100	—	—	—	—	—	3.0
Cebus	25	—	96.4	—	—	—	—	—	3.0
Lagothrix	6	—	67	33	—	—	—	—	3.4
Ateles	16	6	94	—	—	—	—	—	2.9
Brachyteles	1	—	100	—	—	—	—	—	3.0
Macaca	194	2.1	90.3	4	—	—	—	—	3.0
Cynopithecus	4	—	25	75	—	—	—	—	3.8
Papio	50	—	78.4	18	—	—	—	—	3.2
Theropithecus	2	—	100	—	—	—	—	—	3.0
Cercocebus	12	17	75	8	—	—	—	—	2.9
Cercopithecus	37	—	95	5	—	—	—	—	3.1
Erythrocebus	1	—	100	—	—	—	—	—	3.0
Semnopithecus	116	4.1	94	1	—	—	—	—	3.0
Nasalis	49	—	92	8	—	—	—	—	3.1
Colobus	6	—	100	—	—	—	—	—	3.0
Hylobates	318	—	2.1	40.2	50.1	4	—	—	4.6
Symphalangus	17	—	—	29	71	—	—	—	4.7
Pongo	114	—	—	4	57.1	36	2	—	5.4
Pan	92	—	—	—	38.3	52.1	6	—	5.7
Gorilla	60	—	—	2	33.2	58	3	2	5.7
Homo	92	—	—	1	70	28	1	—	5.3

from 2 to 8 in individual cases and the modal number varies between 3 and 6, as shown by table 4. In the great majority of primate genera the modal number is 3. This number has become increased to 5 or even 6 in only two groups of primates, namely in the Lorisinae of the suborder Lemuroidea and in all the higher primates of the suborder Simiae.[8] This is a clear instance of convergent evolution, inasmuch as the same phylogenetic trend to increase the number of sacral segments has affected independently two widely separated groups of primates. It also is noteworthy that among the genera which have acquired the highest numbers of sacral vertebrae one finds the greatest intrageneric variability in this character. Thus, in *Perodicticus* and in *Gorilla*, with average numbers of sacral vertebrae of 6.1 and 5.7, respectively, the ranges of individual variations extend over 5 vertebrae, whereas in all the many genera with modal numbers of only 3 or 4 the ranges of variations include at most 3 segments.

An increase in the number of vertebrae participating in the formation of the sacrum can occur at the expense of the lumbar as well as of the caudal region, as will be discussed later. Figure 2 shows some instances of unilateral transformation of a lumbar into a sacral vertebra. In these three cases (*C*, *G*, *I*) the modal number of lumbar vertebrae is reduced by half a segment; it can be assumed, therefore, that in these specimens the sacral region encroached on the lumbar, rather than vice versa. The assimilation of the first caudal vertebra into the sacrum involves comparatively little change in many genera, as is clearly apparent from some cases shown in figure 2, particularly the examples *D*, *E*, and *I*, in which the last sacral segment most probably has been derived from the caudal region. In the specimens *F* and *G* in figure 2, the first caudal vertebrae came very near to forming sacral foramina together with the last true sacral segments. In spite of the frequent lack of a profound distinction between the last sacral and the first caudal vertebra, transitional, asymmetrical vertebrae are comparatively rare at the caudal end of the sacrum, having been encountered in a total of only 8 cases.

TABLE 5

AVERAGES AND RANGES OF VARIATIONS OF THE NUMBER OF CAUDAL VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Aver.	Range	Genus	Specimens	Aver.	Range
Lemur	3	27.0	26–28	Cebus	12	23.7	22–26
Myoxicebus	1	28.0	—	Lagothrix	1	24.0	—
Lepidolemur	2	21.5	18–25	Ateles	10	31.0	28–34
Microcebus	1	25.0?	—				
Loris	1	5.0	—	Macaca	142	19.1	5–28
Nycticebus	3	7.0	4–9	Cynopithecus	2	11.5	11–12
Perodicticus	4	10.9	9–14	Papio	20	19.7	8–26
Galago	7	25.7	24–27	Cercocebus	6	24.8	23–26
Tarsius	2	28.0	27–29	Cercopithecus	11	26.4	18–29
				Semnopithecus	86	27.7	18–31
Hapale	1	30.0	—	Nasalis	46	24.6	23–26
Oedipomidas	22	32.0	30–34	Colobus	6	26.0	25–28
Leontocebus	1	33.0	—	Hylobates	311	2.7	0–6
Callicebus	2	25.5	25–26	Symphalangus	16	2.4	1–4
Aotus	5	26.0	24–31	Pongo	109	2.6	1–5
Pithecia	2	23.5	22–25	Pan	85	3.2	2–5
Alouatta	9	27.3	26–28	Gorilla	36	3.0	2–5
Saimiri	3	26.7	25–28	Homo	44	3.8	2–5

[8] Sixty-seven chimpanzees, recorded by A. W. Todd, have an average number of 5.4 sacral vertebrae (range = 5 to 6), with the modal number of 5 occurring in 55 per cent. Among 174 gorillas, studied by Randall (1944), the number of sacral vertebrae averages 5.4 (range = 5 to 7) and the modal number of 5 exists in 57.5 per cent. These data may not be strictly comparable to those of the writers since it is particularly in regard to sacral vertebrae that definitions and methods of interpretation are at variance.

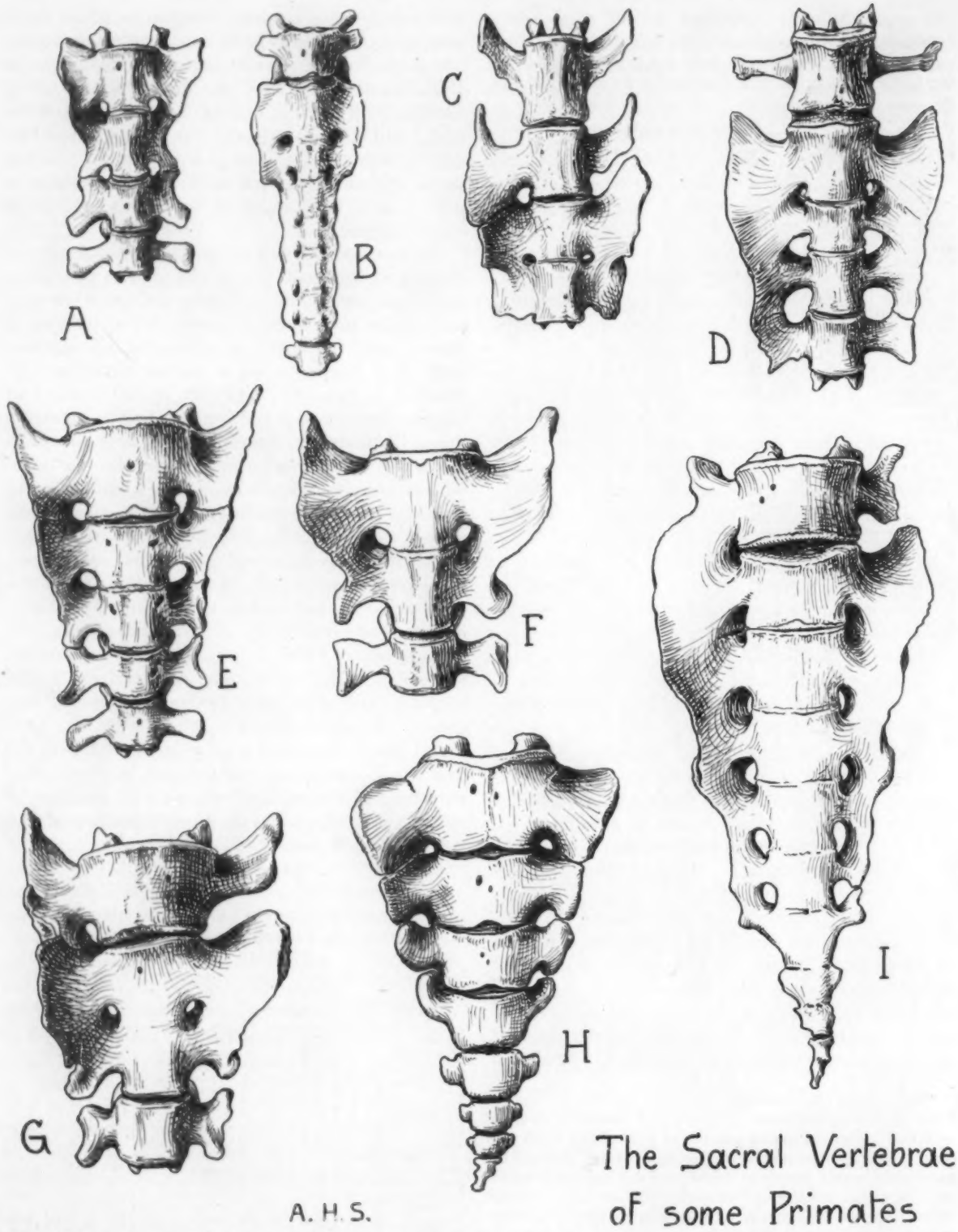


FIG. 2. Examples of variations in the sacral vertebrae of primates. *A* = *Galago*, 3 sacral vertebrae; *B* = *Nycticebus*, 7 sacral v.; *C* = *Oedipomidas*, 2½ sacral v.; *D* = *Alouatta*, 4 sacral v.; *E* = *Cercocebus*, 4 sacral v.; *F* = *Cercocebus*, 2 sacral v.; *G* = *Macaca*, 2½ sacral v.; *H* = *Gorilla*, 4 sacral v.; *I* = *Pan*, 6½ sacral v. All specimens are adult, except *H*, which is infantile. Illustrations of sacral variations in *Hylobates* have been published in a paper by Schultz (1944).

CAUDAL VERTEBRAE

The caudal region of the primate spinal column contains anywhere from none to as many as 34 vertebrae according to the data in table 5. This is by far the most variable of all the spinal regions and the number of its segments has increased or decreased phylogenetically with apparent ease and rapidity since even closely allied species may differ widely in the number of caudal segments. For instance, the Barbary ape and the Celebes macaques possess only very few tail vertebrae,[9] whereas the crab-eating macaques have anywhere from 21 to 28 (table 12).

It may be assumed, as a point of departure, that in the ancestral forms of the primates the tail consisted quite approximately of 25 segments. In a specimen of the tree shrew *Tupaia*, examined by the writers, there are 24 of these vertebrae. Lyon (1913) found 24, 27, and 28 caudal vertebrae, respectively, in 3 skeletons of *Tupaia* and 22 in a specimen of *Tana*. Flower (1884) recorded 26 of these vertebrae in a *Tupaia*. Among still other tree shrews the caudal region contains 27 segments in a *Dendrogale* (Davis, 1938) and 31 or 33 segments in specimens of *Ptilocercus* (Jentink, 1885; Gregory, 1913; Clark, 1926). Among the prosimians the number of caudal segments averages between 21 and 28, except in the specialized Lorisinae and in *Indris*.[10] Evolutionary additions to the number of tail vertebrae have occurred at least in the genera *Hapale*, *Oedipomidas*, and *Ateles* among the New World monkeys and in some species of langurs and guenons among the Old World monkeys. Phylogenetic trends toward marked reduction of tail vertebrae can be clearly recognized in the subfamily Lorisinae and the genus *Indris* among the prosimians, in the genus *Cacajao*[11] among the platyrrhines, in the genus *Cynopithecus* and various species of macaques and baboons among the lower catarrhines, and in all forms of the higher primates. The evolutionary degeneration of the caudal region has attained its extreme in the Asiatic man-like apes—the gibbons, siamangs, and orang-utans. As shown by table 6, among the latter primates there are specimens with only 1 coccygeal vertebra and in one case (seen in the flesh) the coccyx even has disappeared completely. The caudal region of man has become reduced to a lesser degree than that of any of the man-like apes. The average number of coccygeal vertebrae in man equals 4.2 in 745 cases collected from the literature (Schultz, 1930), hence the corresponding average (3.8) for the small series in table 5 appears to be exceptionally low.

In the genus *Hylobates* the modal number of 3 coccygeal segments exists in only 38 per cent of all specimens and individual deviations from this number occur in nearly two-thirds of the cases, extending over a total range of 7 vertebrae (table 6). This represents a remarkable variability, greatly in excess of the variabilities found in the other spinal regions. There can be little doubt that these exceedingly common numerical variations in coccygeal vertebrae are connected with the profound evolutionary change in the tail region of higher primates and they might also be regarded as potential stepping stones for further change.

TABLE 6

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF COCCYGEAL VERTEBRAE IN THE HIGHER PRIMATES

Genus	Specimens	Number of Coccygeal Vertebrae						
		0	1	2	3	4	5	6
Hylobates	311	1	5	37	**38**	15	3	1
Symphalangus	16	—	6	**50**	38	6	—	—
Pongo	109	—	5	38	**47**	9	1	—
Pan	85	—	—	15	**54**	24	7	—
Gorilla	36	—	—	31	**47**	17	5	—
Homo	44	—	—	2	27	**55**	16	—

COMBINATIONS OF VARIATIONS

PRESACRAL VERTEBRAE

The individual combinations of numerical variations in the vertebrae of the different spinal

[9] Mivart (1865) found 3 caudal vertebrae in one Barbary ape and 4 in two other specimens. According to Giebel and Leche (1874–1900) the Barbary ape has 4 tail segments, whereas A. W. Todd records only 2 of these vertebrae in a specimen of the same species (*Macaca sylvanus*). A skeleton of a Celebes macaque (*Macaca maurus*), examined by the writers, contains 5 caudal vertebrae.

[10] Mivart (1865) found 14 caudal vertebrae in an indris, Flower (1884) 9, and Speransky (1926) 11. According to the data of A. W. Todd, three skeletons of *Indris indris* have 7, 9, and 11 caudal segments, respectively. Giebel and Leche (1874–1900) list 9 to 14 caudal vertebrae in "*Lichanotus brevicaudatus*," which is an old term for the indris. For the closely related avahi, Flower (1885) gives the number of caudal vertebrae as 23.

[11] The number of caudal vertebrae in *Cacajao* (= "*Brachyurus*") is given as 18 by Flower (1862), as 17 by Mivart (1865) and by Giebel and Leche (1874–1900), and as 15 to 20 by Weber (1927–1928).

regions are of great significance in elucidating the nature of the regional variations which have been dealt with in the preceding chapters.

As stated earlier, variations in the number of cervical vertebrae are very rare among primates. An increase in this number, to 8, could be recorded here for only one specimen, a gibbon, which possesses 13 thoracic vertebrae, or precisely the modal number for this particular genus. A decrease in the number of cervical vertebrae, to only 6, exists in a total of 7 specimens. Among the latter, the macaque possesses 13 thoracic segments, or one more than the modal number (12) of this genus. Two of the three gibbons with only 6 cervical segments have 13 and the third has 14 thoracic vertebrae, the mode being 13. One orang-utan has 12 and another 13 thoracic vertebrae, the mode equalling 12. Fi-

TABLE 7

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF THORACIC + LUMBAR VERTEBRAE AND AVERAGE NUMBERS OF THESE VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Number of Thoracic + Lumbar Vertebrae										Average
		15	16	17	18	19	20	21	22	23	24	
Daubentonia	2	—	—	—	—	**100**	—	—	—	—	—	19.0
Lemur	21	—	—	—	14	**81**	5	—	—	—	—	18.9
Myoxicebus	4	—	—	—	25	**50**	25	—	—	—	—	19.0
Lepidolemur	3	—	—	—	—	—	—	**67**	33	—	—	21.3
Microcebus	5	—	—	—	—	20	**80**	—	—	—	—	19.8
Chirogale	2	—	—	—	—	—	**100**	—	—	—	—	20.0
Lichanotus	3	—	—	—	—	—	**100**	—	—	—	—	20.0
Loris	6	—	—	—	—	—	—	—	17	**67**	16	23.0
Nycticebus	8	—	—	—	—	—	—	—	13	12 **38**	37	23.2
Perodicticus	11	—	—	—	—	—	18	27	**37**	9 9	—	21.5
Galago	18	—	—	—	—	**72**	6 22	—	—	—	—	19.3
Tarsius	7	—	—	—	—	**100**	—	—	—	—	—	19.0
Hapale	9	—	—	—	11	**78**	11	—	—	—	—	19.0
Oedipomidas	57	—	—	—	—	2 **96**	2	—	—	—	—	19.0
Leontocebus	4	—	—	—	—	**100**	—	—	—	—	—	19.0
Callicebus	2	—	—	—	—	50	**50**	—	—	—	—	19.5
Aotus	7	—	—	—	—	—	—	**100**	—	—	—	21.0
Pithecia	2	—	—	—	—	**100**	—	—	—	—	—	19.0
Cacajao	1	—	—	—	—	**100**	—	—	—	—	—	19.0
Alouatta	21	—	—	—	—	**76**	24	—	—	—	—	19.2
Saimiri	5	—	—	—	—	—	**100**	—	—	—	—	20.0
Cebus	25	—	—	—	4	32	4 **60**	—	—	—	—	19.6
Lagothrix	6	—	—	17	**50**	33	—	—	—	—	—	18.2
Ateles	16	—	—	—	**87**	13	—	—	—	—	—	18.1
Brachyteles	1	—	—	—	**100**	—	—	—	—	—	—	18.0
Macaca	196	—	—	—	4	1 **89**	2 4	—	—	—	—	19.0
Cynopithecus	4	—	—	—	25	**75**	—	—	—	—	—	18.8
Papio	52	—	—	—	4	**96**	—	—	—	—	—	19.0
Theropithecus	2	—	—	—	—	**100**	—	—	—	—	—	19.0
Cercocebus	12	—	—	—	17	**83**	—	—	—	—	—	18.8
Cercopithecus	37	—	—	—	5	**89**	6	—	—	—	—	19.0
Erythrocebus	1	—	—	—	—	**100**	—	—	—	—	—	19.0
Semnopithecus	119	—	—	—	5	1 **92**	2	—	—	—	—	19.0
Nasalis	49	—	—	—	2	**98**	—	—	—	—	—	19.0
Colobus	6	—	—	—	17	**83**	—	—	—	—	—	18.8
Hylobates	318	—	—	4	1 **70**	2 23	—	—	—	—	—	18.2
Symphalangus	17	—	6	**53**	41	—	—	—	—	—	—	17.4
Pongo	120	20	1 **71**	1 7	—	—	—	—	—	—	—	15.9
Pan	93	—	22	5 **73**	—	—	—	—	—	—	—	16.8
Gorilla	58	—	40	3 **55**	2	—	—	—	—	—	—	16.6
Homo	109	—	8	**89**	3	—	—	—	—	—	—	16.9

nally, the human skeleton with only 6 cervical vertebrae has 12 thoracic, which corresponds to the human norm. It is seen by these examples that deviations from the average number of cervical vertebrae are combined either with average numbers of thoracic vertebrae, or else with deviations from the latter average in the direction opposite to the deviations in the cervical region. In other words, the cervical region can lose a segment to the profit of the thoracic region or the latter remains unaffected by variations in the former, but an increase in cervical vertebrae is not accompanied by an increase in thoracic vertebrae, nor does a decrease in the former ever concur with a decrease in the latter.

The total number of vertebrae in the combined thoracic and lumbar regions varies among primates in individual cases between 15 and 24, as shown by table 7. Among the tree shrews examined for this study, the number of thoracic + lumbar vertebrae equals 19 in one specimen of *Tana* and in 10 specimens of *Tupaia*, while in another *Tupaia* this number is 18. Nineteen thoracic + lumbar vertebrae seem to represent the rule for other Tupaiidae as well, for this is the number found in *Dendrogale* by Davis (1938) and in *Ptilocercus* by Jentink (1885), Gregory (1913), and Clark (1926). It seems most likely that the primitive, original number of these vertebrae in primates was 19 (see also Todd, 1922), of which 13 were thoracic and 6 lumbar. This total number of 19 has been retained unaltered by many more genera than have the primitive numbers of 13 thoracic or of 6 lumbar vertebrae, showing that the lumbo-sacral border phylogenetically is more stable than the thoraco-lumbar border. A modal number of 19 thoracic + lumbar vertebrae is characteristic of many prosimians and platyrrhines and of all catarrhine monkeys. Increases in this modal number have occurred in a variety of genera among the Lemuroidea and in some New World monkeys, but not in a single catarrhine genus. Such increases have reached the greatest extreme in the subfamily Lorisinae, among which the pelvic girdle has shifted for as many as 4 and even 5 segments in a caudal direction. The opposite evolutionary trend, i. e., a migration of the sacrum in a cranial direction, has affected the American subfamily Atelinae and all the higher primates. The modal number of the thoracic + lumbar vertebrae has decreased to 18 in gibbons, to 17 in siamangs, the African apes,[12] and man, and to even only 16 in orang-utans. Among the latter, one finds specimens with but 15 thoracic + lumbar segments, which is the most extreme phylogenetic reduction in presacral vertebrae among primates. It can be seen from the data in table 7 that the ranges of intrageneric variations in the numbers of these vertebrae extend over only 3 segments or less, with the single exception of the genus *Perodicticus*.

The numerical variations in the thoracic and in the lumbar vertebrae combine in many different manners to form the variable total number of these vertebrae, as is shown by the examples in figure 3. In macaques, e. g., the combination of 12 thoracic and 7 lumbar vertebrae exists in 78 per cent of the cases. In 13 per cent of the specimens one still encounters the primitive combination of 13 thoracic and 6 lumbar vertebrae. In another 4 per cent of macaques the total number of these vertebrae has been reduced to 18 by the combination of 12 thoracic and 6 lumbar segments and in the remaining 5 per cent the total has increased to 20 by combining either 13 thoracic with 7 lumbar vertebrae or 12 thoracic with 8 lumbar. The most noteworthy conclusion, based on figure 3, is the fact that an increase in the modal number of thoracic vertebrae of a given genus never is combined with an increase in the modal number of lumbar vertebrae of the same genus, but only with the latter mode itself or else with a decrease in this modal number. Correspondingly, a decreased number of thoracic vertebrae never is accompanied by a decrease in the number of lumbar vertebrae typical of a given genus. This finding demonstrates the definite, though limited, interdependence of these variations, inasmuch as fluctuations in the number of thoracic segments either have no effect on the lumbar series or else are combined with numerical deviations in lumbar segments in an opposite and never in the same direction as in the thoracic region. Unfortunately, the general validity of these conclusions could not be tested on the basis of series of platyrrhine and prosimian primates, since the latter series are too limited for this kind of analysis.

PRECAUDAL VERTEBRAE

The numbers of vertebrae in the precaudal regions of the spine combine to a total of 29 in all

[12] For 68 chimpanzees, A. W. Todd obtained an average of 16.8 thoracic + lumbar vertebrae (range = 16 to 17), the modal number of 17 being present in 84 per cent.

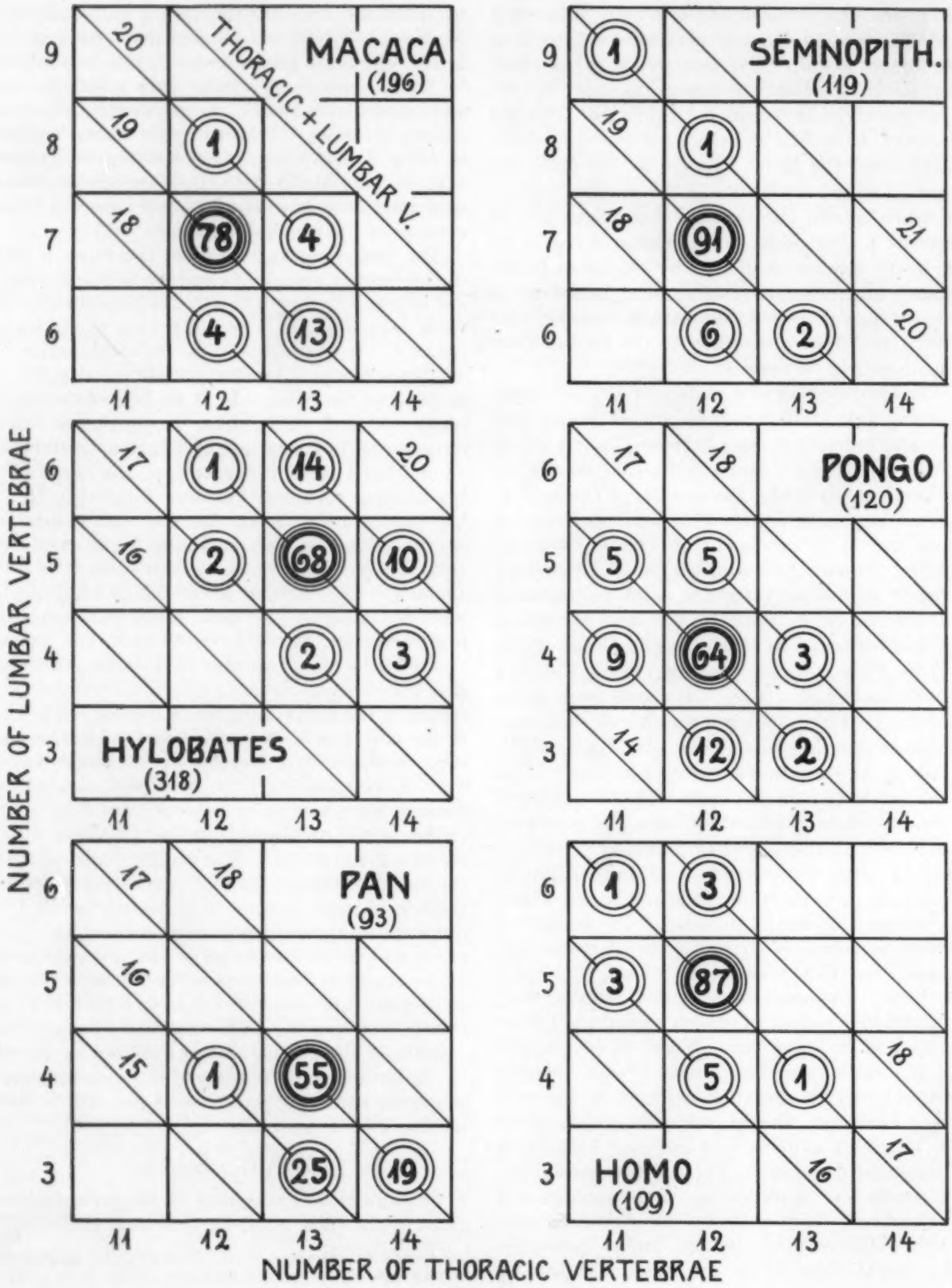

MACACA
(196)
THORACIC + LUMBAR V.
SEMNOPITH.
(119)
HYLOBATES
(318)
PONGO
(120)
PAN
(93)
HOMO
(109)
NUMBER OF LUMBAR VERTEBRAE
NUMBER OF THORACIC VERTEBRAE

FIG. 3.

TABLE 8

PERCENTAGE DISTRIBUTION OF VARIATIONS IN THE NUMBER OF PRECAUDAL VERTEBRAE AND AVERAGE NUMBERS OF THESE VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Number of Precaudal Vertebrae												Average
		27	28	29	30	31	32	33	34	35	36	37	38	
Daubentonia	2	—	—	**100**	—	—	—	—	—	—	—	—	—	29.0
Lemur	20	—	25	5 **65**	5	—	—	—	—	—	—	—	—	28.8
Myoxicebus	4	—	25	**50**	25	—	—	—	—	—	—	—	—	29.0
Lepidolemur	3	—	—	—	—	33	**34**	33	—	—	—	—	—	32.0
Microcebus	5	—	—	40	**60**	—	—	—	—	—	—	—	—	29.6
Chirogale	1	—	—	—	**100**	—	—	—	—	—	—	—	—	30.0
Lichanotus	3	—	—	—	33	33 **34**	—	—	—	—	—	—	—	30.5
Loris	4	—	—	—	—	—	—	25	25	**25**	25	—	—	34.5
Nycticebus	6	—	—	—	—	—	—	—	—	17	**33**	33	17	36.5
Perodicticus	11	—	—	—	—	9	—	—	27	**37** 9	—	9	9	— 34.6
Galago	17	—	—	**94**	6	—	—	—	—	—	—	—	—	29.1
Tarsius	6	—	—	**100**	—	—	—	—	—	—	—	—	—	29.0
Hapale	8	—	25	**75**	—	—	—	—	—	—	—	—	—	28.8
Oedipomidas	57	—	2	**96**	2	—	—	—	—	—	—	—	—	29.0
Leontocebus	3	—	33	**67**	—	—	—	—	—	—	—	—	—	28.7
Callicebus	2	—	—	50	**50**	—	—	—	—	—	—	—	—	29.5
Aotus	6	—	—	—	—	**100**	—	—	—	—	—	—	—	31.0
Pithecia	2	—	—	**100**	—	—	—	—	—	—	—	—	—	29.0
Cacajao	1	—	—	—	**100**	—	—	—	—	—	—	—	—	30.0
Alouatta	20	—	—	**65**	25	10	—	—	—	—	—	—	—	29.5
Saimiri	5	—	—	—	**100**	—	—	—	—	—	—	—	—	30.0
Cebus	25	—	4	32	**64**	—	—	—	—	—	—	—	—	29.6
Lagothrix	6	—	**50**	50	—	—	—	—	—	—	—	—	—	28.5
Ateles	16	6	**81**	13	—	—	—	—	—	—	—	—	—	28.1
Brachyteles	1	—	**100**	—	—	—	—	—	—	—	—	—	—	28.0
Macaca	193	—	6	**84** 1	9	—	—	—	—	—	—	—	—	29.2
Cynopithecus	4	—	—	**50**	50	—	—	—	—	—	—	—	—	29.5
Papio	50	—	2	**78** 4	16	—	—	—	—	—	—	—	—	29.2
Theropithecus	2	—	—	**100**	—	—	—	—	—	—	—	—	—	29.0
Cercocebus	12	—	25	**75**	—	—	—	—	—	—	—	—	—	28.8
Cercopithecus	36	—	3	**89**	8	—	—	—	—	—	—	—	—	29.1
Erythrocebus	1	—	—	**100**	—	—	—	—	—	—	—	—	—	29.0
Semnopithecus	116	—	8	**91**	1	—	—	—	—	—	—	—	—	28.9
Nasalis	49	—	—	**94**	6	—	—	—	—	—	—	—	—	29.1
Colobus	6	—	17	**83**	—	—	—	—	—	—	—	—	—	28.8
Hylobates	318	1	1	33	**52**	13	1	—	—	—	—	—	—	29.8
Symphalangus	17	—	6	**82**	12	—	—	—	—	—	—	—	—	29.1
Pongo	114	11	**61**	24	4	—	—	—	—	—	—	—	—	28.2
Pan	92	—	4	**51** 1	41	2	—	—	—	—	—	—	—	29.4
Gorilla	57	—	9	**58**	32	2	—	—	—	—	—	—	—	29.3
Homo	88	—	3	**74**	22	1	—	—	—	—	—	—	—	29.2

FIG. 3. Diagrammatic representation of the percentage distribution of combinations of variations in the numbers of thoracic and of lumbar vertebrae in the 6 genera for which the largest series of specimens have been available. The figures in the circles show the percentages of the cases with a given combination of variations. The highest percentage frequency of all existing combinations in a genus is encircled 3 times. The diagonal lines and the figures above them indicate the total number of thoracic and lumbar vertebrae in the combinations of variations. For these diagrams half thoracic vertebrae have been counted as full vertebrae and half lumbar vertebrae have been ignored; e. g., 12½ thoracic v. figure here as 13 and 4½ lumbar v. as 4, the sum of the figures remaining 17. The figures in parentheses represent the number of specimens used in the construction of each diagram.

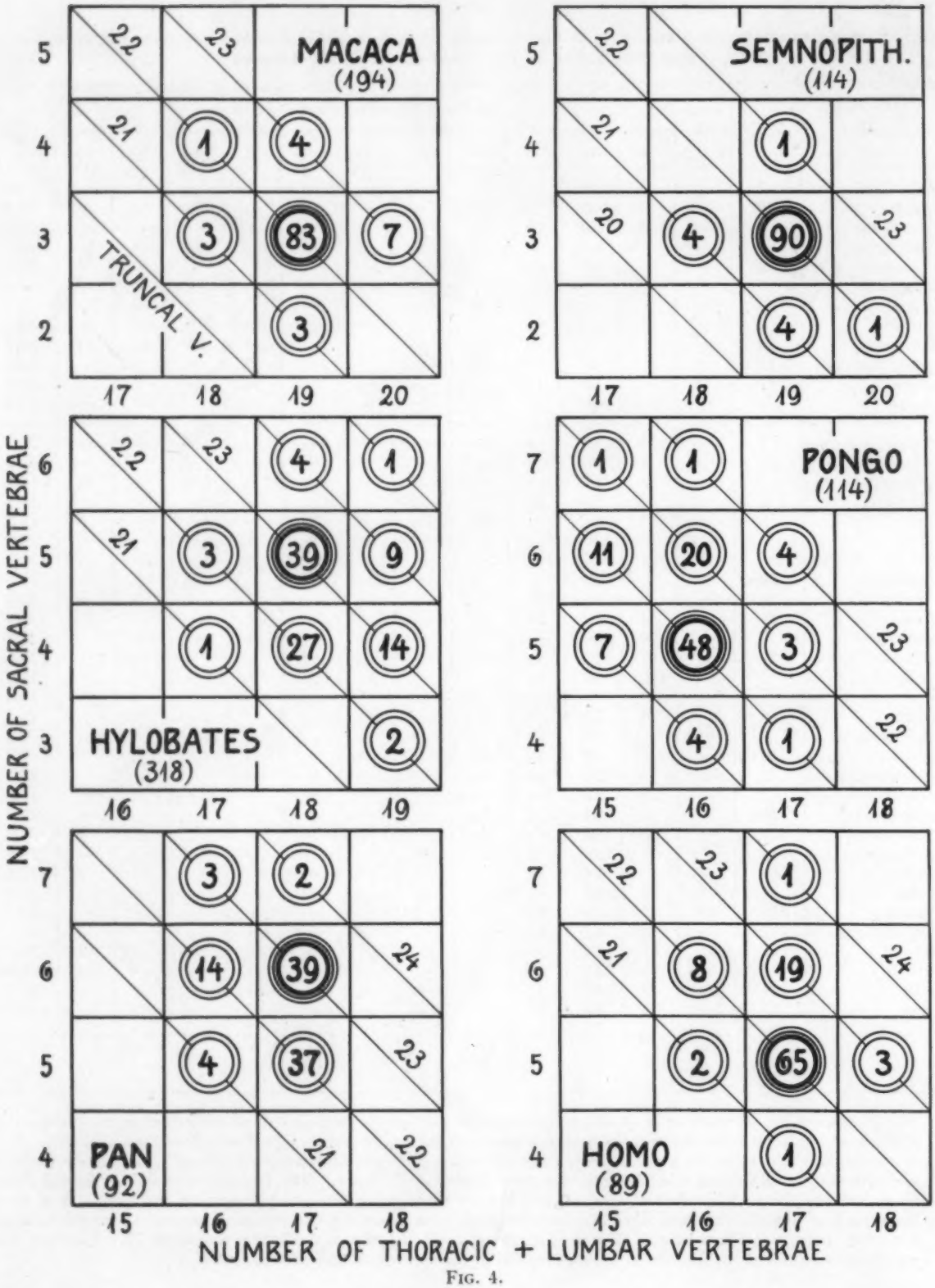

MACACA
(194)
TRUNCAL V.
SEMNOPITH.
(114)
HYLOBATES
(318)
PONGO
(114)
PAN
(92)
HOMO
(89)
NUMBER OF SACRAL VERTEBRAE
NUMBER OF THORACIC + LUMBAR VERTEBRAE

FIG. 4.

the 12 tree shrews examined by the authors.[13] This corresponds to the total of the assumed original 7 cervical, 13 thoracic, 6 lumbar, and 3 sacral vertebrae. Among the recent primates, 29 precaudal vertebrae have persisted as modal number in the great majority of genera, as is shown by the data in table 8. Increases in the number of precaudal segments have occurred in several genera of the family Lemuridae and in all available genera of the subfamily Lorisinae. Among the latter there are found as many as 38 precaudal vertebrae and the total varies intragenerically to an unusual degree, a frequent accompaniment of extreme phylogenetic change. The unique rise in the number of precaudal segments in the Lorisinae is due to the combination of phylogenetic increases in the numbers of thoracic + lumbar and of sacral vertebrae. On the other hand, the comparatively slight increases in the number of precaudal segments in various platyrrhines are caused exclusively by additions to the series of thoracic and lumbar vertebrae. Decreases in the modal number of precaudal vertebrae are encountered only in the platyrrhine subfamily Atelinae and in orangutan, and these phylogenetic reductions are entirely due to numerical decreases in the thoracic and lumbar series. In the siamang, the African great apes, and man, the evolutionary decrease in thoracic and lumbar segments is, on an average, compensated for by the phylogenetic increase in sacral vertebrae with the result that the caudal series begins with the thirtieth segment, just as in original, ancestral forms. In the gibbon, finally, the addition to the sacral region has so far exceeded the subtraction from the presacral regions that the precaudal series has risen to 30 segments. The generic averages of the numbers of precaudal vertebrae range among prosimians between 28.8 and 36.5, whereas in the simian suborder only between 28.2 and 31.0.[14] The latter range is remarkably small, considering that these figures represent the combinations of variations in four regions of the spine.

Figure 4 shows the combinations of individual variations in the numbers of thoracic + lumbar and of sacral vertebrae for the 6 genera for which the largest series of specimens are available. In macaques, e. g., the modal number of 22 truncal vertebrae is formed by the combination of 19 thoracic + lumbar with 3 sacral segments in 83 per cent of all cases and by the combination of 18 of the former with 4 of the latter in 1 per cent. An increase in truncal vertebrae to 23 results from the combination of either 19 thoracic + lumbar segments with 4 sacral ones (4 per cent of cases) or 20 thoracic + lumbar vertebrae with 3 sacral ones (7 per cent). Only 21 truncal vertebrae, finally, contain among macaques either 19 thoracic + lumbar and 2 sacral segments (3 per cent) or 18 of the former and 3 of the latter (3 per cent). In no case has there been found an increase in thoracic + lumbar segments combined with an increase in sacral ones, nor a decrease in the former combined with a decrease in the latter. A deviation from the modal number of sacral vertebrae can be accompanied by a deviation in the opposite direction from the modal number of thoracic + lumbar vertebrae or may leave the latter number unaltered, but intragenerically there never are combined increases with increases or decreases with decreases in the numbers of sacral and of thoracic + lumbar vertebrae. The same holds true in regard to langur and to man, but among the three anthropoid apes dealt with in figure 4 there do occur some few exceptions to this rule.

That there exists a limited inverse relation between the number of sacral vertebrae and the numbers of vertebrae in the adjoining spinal regions is demonstrated by the following data: In the genus *Hylobates* the (142) specimens with fewer than 5 sacral vertebrae have on an average 18.32 thoracic + lumbar vertebrae, the (160) specimens with 5 sacral vertebrae have a corresponding average of 18.11, and in the (16) specimens with more than 5 sacral vertebrae this

[13] These comprise 11 *Tupaia* and 1 *Tana*. There also are 29 precaudal vertebrae in another specimen of *Tupaia*, listed by Lyon (1913) (the other tree shrews recorded by Lyon have been examined by the writers), in a skeleton of *Dendrogale* (Davis, 1938), and in *Ptilocercus* (Jentink, 1885; Clark, 1926).

[14] The average number of precaudal segments in the 62 chimpanzees studied by A. W. Todd equals 29.3 (range = 28 to 30) and the modal number of 29 occurs in 65 per cent.

FIG. 4. Diagrammatic representation of the percentage distribution of combinations of variations in the numbers of sacral and of thoracic + lumbar vertebrae in six genera. The diagonal lines and the figures above them indicate the total number of truncal vertebrae (= thoracic + lumbar + sacral vertebrae) in the combinations of variations. For these diagrams, half thoracic + lumbar vertebrae have been counted as full vertebrae and half sacral vertebrae have been ignored. For other explanations, see title of figure 3.

figure has dropped to 18.06. In the genus *Pongo* the (5) specimens with fewer than 5 sacral vertebrae possess on an average 16.20 thoracic + lumbar vertebrae, the (65) specimens with 5 sacral vertebrae have only 15.92 of these vertebrae, and in the remaining (44) specimens with more than 5 sacral vertebrae the number of thoracic + lumbar segments has further decreased to 15.78. The number of sacral vertebrae also inversely influences the number of coccygeal segments, as is evident from the following examples: In the (139) gibbons with fewer than 5 sacral vertebrae there are on an average 2.91 coccygeal vertebrae, in the (156) gibbons with 5 sacral segments the corresponding value equals 2.69, and in the (16) gibbons with more than 5 sacral vertebrae even only 1.75. In orang-utans the number of coccygeal elements averages 2.75 in (only 4) specimens with fewer than 5 sacral vertebrae, 2.82 in (62) specimens with 5 sacral vertebrae, and only 2.32 in (43) specimens with more than 5 sacral vertebrae. It is clearly seen that a gain in the number of sacral vertebrae is not accompanied by an equally large loss in the number of presacral or in that of coccygeal segments, but only by a much smaller decrease in the latter numbers. Again it can be concluded, therefore, that changes in the number of sacral vertebrae can occur through transformation of segments at the lumbo-sacral or sacro-caudal border, but they also can take place without affecting the numbers of segments in the presacral or postsacral series. The data, given above, permit the additional conclusion that, generally, there exists a somewhat closer inverse relation between the number of sacral and that of coccygeal vertebrae than between the number of sacral and that of presacral vertebrae. This, in turn, implies that a last sacral segment is more frequently and readily changed into a first coccygeal vertebra, or vice versa, than a first sacral vertebra is transformed into a last lumbar vertebra, or vice versa.

TOTAL NUMBER OF VERTEBRAE

The total number of vertebrae is influenced above all by the variable number of segments in the caudal region. It is the latter spinal portion which has undergone far more profound and frequent phylogenetic alterations than has any of the other vertebral regions. In consequence, the total number of vertebrae varies very extensively among primates and even within single genera. In the material examined for this study, this total ranges individually from 29 to 63, as shown by table 9. Among the prosimians the total number of vertebrae most often lies well above 50 and probably has changed but little during evolution, as it may be assumed that the primitive, original total number equalled approximately 54. In a specimen of the tree shrew, *Tupaia*, examined by the writers, this total is 53. Lyon (1913) records 53, 56, and 57, respectively, for the total number of vertebrae in three skeletons of *Tupaia*, and 51 in a specimen of *Tana*. Flower (1884) counted 55 vertebrae in another *Tupaia* and Davis (1938) 56 in a *Dendrogale*. In *Ptilocercus* this total amounts to 60 according to both Jentink (1885) and Clark (1926). The lowest totals of all lemuroids exist in the subfamily Lorisinae, which combine exceptionally high numbers of precaudal vertebrae with very much reduced numbers of caudal segments. Among simian primates, the largest totals are encountered in the Hapalidae and in *Ateles* and this on account of the great number of segments in their highly developed tails. The smallest of all totals occur in the entire group of higher primates, all of which have shared the marked evolutionary trend to reduce the number of spinal segments. It is noteworthy that man has not attained the extreme degree of this reduction and that the man-like apes [15] possess smaller averages for the total number of vertebrae.

TABLE 9

AVERAGES AND RANGES OF VARIATIONS OF THE TOTAL NUMBER OF VERTEBRAE IN THE DIFFERENT PRIMATE GENERA

Genus	Specimens	Aver.	Range	Genus	Specimens	Aver.	Range
Lemur	2	56.0	55–57	Cebus	12	53.1	50–56
Myoxicebus	1	56.0	—	Lagothrix	1	52.0	—
Lepidolemur	2	53.5	51–56	Ateles	10	59.1	56–62
Microcebus	1	55.0?	—				
Loris	1	38.0	—	Macaca	142	48.1	35–57
Nycticebus	3	43.7	41–47	Cynopithecus	2	41.0	41–41
Perodicticus	4	46.0	44–48	Papio	20	48.8	38–55
Galago	7	54.7	53–56	Cercocebus	6	53.5	52–55
Tarsius	2	57.0	56–58	Cercopithecus	11	55.5	47–58
				Semnopithecus	86	56.6	47–60
Hapale	1	58.0	—	Nasalis	46	53.7	52–55
Oedipomidas	22	61.0	59–63	Colobus	6	54.8	53–57
Leontocebus	1	62.0	—	Hylobates	311	32.5	30–36
Callicebus	2	55.5	54–57	Symphalangus	16	31.5	30–32
Aotus	5	57.0	55–62	Pongo	111	30.9	29–33
Pithecia	2	52.5	51–54	Pan	85	32.6	31–35
Alouatta	9	56.7	55–58	Gorilla	35	32.2	31–35
Saimiri	3	56.7	55–58	Homo	34	33.1	32–34

[15] In 61 complete gorilla skeletons, studied by Randall (1944), the total number of vertebrae varies between 31 and 35 and averages 32.2. These data, regarding which there can exist no discrepancy in the methods used by different authors, agree perfectly with the figures listed for the gorilla in table 9.

VARIABILITY

The tendency to deviate individually from the modal number of vertebrae differs in degree very widely among primate genera as well as in the various spinal regions. This is demonstrated by the standard deviations listed in table 10. It already has been shown in a previous chapter that the number of cervical vertebrae is extremely stable in primates, so that the standard deviations of this character equal zero or very little more. From the data in table 10 it is evident that in general the numbers of vertebrae in the thoracic, lumbar, and sacral regions have similar variabilities, represented, on an average, by standard deviations amounting to 0.40 to 0.44. In contrast to this, the number of segments in the caudal region and, consequently, the total number of vertebrae are very variable, their standard deviations averaging 1.72 and 1.73, respectively, or approximately four times the corresponding values of the precaudal regions. Naturally, the standard deviations for the number of caudal vertebrae are by far the highest in such genera as *Macaca* and *Papio*, which contain both long- and short-tailed species. But even in such series as those of *Oedipomidas* and *Nasalis*, which are composed exclusively of specimens of a single species, the standard deviations for the number of caudal vertebrae are much higher than those for the numbers of vertebrae in the other regions.

The arithmetic means of the standard deviations for the numbers of truncal vertebrae, listed in the last column of table 10, show most conveniently the marked differences in the variability of these numbers existing among different genera of primates. According to these data, the highly specialized genus *Perodicticus* clearly is the least stable among all primates studied. Even within a single species of potto this variability is amazingly high. Thus, among the 8 available skeletons of *Perodicticus potto* the formulae for the truncal vertebrae alone are not alike in any two specimens. These particular formulae are as follows: $16\frac{1}{2}$–6–7; 16–7–5; 16–6–8; 16–6–6; 16–5–$6\frac{1}{2}$; 15–7–6; 15–6–6; 14–7–6. The most constant form is *Semnopithecus*, in spite of the fact that this genus contains a great number of different taxonomic species which are regarded by various authors as belonging to several distinct genera. Man is very significantly more stable in regard to numerical variations in vertebrae than are the other forms of higher primates. According to the last column in table 10, man has practically the same average standard deviation for the truncal vertebrae as the macaque.

TABLE 10

STANDARD DEVIATIONS FOR THE NUMBERS OF VERTEBRAE IN THE DIFFERENT SPINAL REGIONS IN THE PRIMATE GENERA WITH AT LEAST 10 SPECIMENS IN EACH

Genus	Thor.	Lumb.	Thor. + Lumb.	Sacr.	Precaud.	Caud.	Total Number	½ of Thor. + Lumb. + Sacral
Lemur	0.33	0.44	0.42	0.30	0.51	—	—	0.36
Perodicticus	0.91	1.02	0.92	1.00	1.50	—	—	0.98
Galago	0.41	0.35	0.41	0.38	0.23	—	—	0.38
Oedipomidas	0.48	0.47	0.14	0.06	0.18	1.44	1.38	0.34
Alouatta	0.52	0.35	0.42	0.40	0.67	—	—	0.42
Cebus	0.45	0.55	0.56	0.01	0.56	1.10	1.60	0.34
Ateles	0.24	0.24	0.31	0.24	0.43	1.73	1.75	0.24
Macaca	0.35	0.35	0.29	0.27	0.42	4.29	4.18	0.32
Papio	0.48	0.48	0.19	0.38	0.40	4.75	4.63	0.45
Cercocebus	0.43	0.47	0.37	0.49	0.43	—	—	0.46
Cercopithecus	0.38	0.36	0.32	0.23	0.32	3.02	3.02	0.32
Semnopithecus	0.13	0.32	0.26	0.23	0.28	2.24	2.22	0.23
Nasalis	0.27	0.30	0.14	0.27	0.24	0.79	0.81	0.28
Hylobates	0.38	0.43	0.48	0.61	0.70	0.93	0.90	0.47
Symphalangus	0.38	0.50	0.59	0.45	0.41	0.70	0.61	0.44
Pongo	0.42	0.43	0.51	0.59	0.69	0.76	0.84	0.48
Pan	0.39	0.47	0.41	0.57	0.60	0.78	0.83	0.48
Gorilla	0.38	0.45	0.51	0.63	0.63	0.83	0.89	0.49
Homo	0.21	0.30	0.31	0.50	0.50	0.70	0.58	0.34
Average of Column	0.40	0.44	0.40	0.40	0.51	1.72	1.73	0.41

To be precise, it should be mentioned that the present series for *Macaca* contains a number of different species, and that a single species can show slightly smaller variability. For instance, from the data on 152 vertebral columns of *Macaca mulatta*, published by Zuckerman (1938), a value of 0.30 is obtained for the mean of the standard deviations of the truncal vertebrae, instead of 0.32 which is the value for the less homogeneous series of the writers.

As has been shown in a previous chapter, the numerical variations of vertebrae can combine intragenerically in many different manners. The most frequent combination of numbers of vertebrae represents the statistical norm of a genus. These norms and the percentage frequencies of their occurrence are listed in table 11 for the primate genera in which at least twenty specimens were studied. In man, e. g., the statistical norm for the precaudal vertebrae exists in 62.5 per cent of cases [16] and each of all other combinations of numerical variations in vertebrae is limited to a smaller percentage. The figures in the last column of table 11 demonstrate the striking differences in the percentage frequencies of the norm among the various genera. The highest value exists in *Semnopithecus*, the genus which also had been found to be most constant according to the data in table 10. The lowest values are encountered in the African great apes; and all anthropoid apes are far more variable than man, as judged by the figures in table 11. This great contrast is not largely due to the inclusion of various taxonomic species in some of the anthropoid genera, whereas the genus *Homo* contains but one species. For instance, in the single gibbon species *Hylobates lar* the statistical norm occurs in 92 of 241 specimens examined, i. e., in only 38.2 per cent of the cases, a percentage which lies far below the corresponding value (62.5) for man. It also may be mentioned that the orang-utans from Borneo and those from Sumatra, which are regarded by some authors as distinct species, do not differ significantly in regard to the frequency and distribution of the numerical variations in vertebrae. Hence, even if the orangs from one island alone were to be considered, they would still be a great deal more variable than man in the numbers of their vertebrae.[17] It must be emphasized, however, that many species differences regarding the numerical variations of vertebrae do exist, and that these occur not only in the caudal, but also in the truncal regions of the spine. For instance, in all 8 specimens of *Gorilla beringei* examined there are 16 thoracic + lumbar vertebrae; whereas among the 50 skeletons of *Gorilla gorilla* used here, 16 of these vertebrae are present in only 15 cases and the remaining 35 specimens all possess more than 16 thoracic + lumbar vertebrae, the average of the latter series being 16.7. The number of thoracic vertebrae was found to be 14 in all of the 11 available specimens of *Hylobates gabrielli;* but in the 16 specimens of *H. concolor* and in the 5 specimens of *H. hoolock* which have been studied only 12 or 13 thoracic vertebrae could be recorded, the average number of the former series amounting to 12.9 and that of the latter to 12.6. Among the available skele-

TABLE 11

PERCENTAGE FREQUENCY OF OCCURRENCE OF STATISTICAL NORM FOR THE NUMBERS OF CERVICAL, THORACIC, LUMBAR, AND SACRAL VERTEBRAE IN THE PRIMATE GENERA WITH AT LEAST 20 SPECIMENS IN EACH

Genus	Specimens	Statistical Norm				Present in Per Cent of Cases
		Cerv.	Thor.	Lumb.	Sacr.	
Lemur	20	7	12	7	3	55.0
Oedipomidas	57	7	12	7	3	59.6
Alouatta	20	7	14	5	3	60.0
Cebus	24	7	14	6	3	54.2
Macaca	193	7	12	7	3	71.5
Papio	50	7	12	7	3	46.0
Cercopithecus	36	7	12	7	3	75.0
Semnopithecus	116	7	12	7	3	88.8
Nasalis	49	7	12	7	3	85.7
Hylobates	318	7	13	5	5	36.5
Pongo	115	7	12	4	5	40.0
Pan	92	7	13	4	6	29.3
Gorilla	57	7	13	4	6	28.1
Homo	88	7	12	5	5	62.5

[16] In larger series of cases this figure usually is somewhat higher, at least according to the literature. Thus, among the published records for 493 human spines, collected by Schultz (1930), the statistical norm for the truncal vertebrae was found in 71.2 per cent of cases. The inclusion of the cervical vertebrae would not have lowered this value to a significant extent.

[17] The chimpanzee material of the Hamann Museum, studied by A. W. Todd, comes almost exclusively from one limited district in West Africa. This series is less variable than the chimpanzee series of the writers. According to Todd's data, the statistical norm (7–13–4–5) exists in 48.4 per cent of 62 specimens. The greater stability of the numbers of vertebrae in Todd's series cannot be due entirely to differences in methods, such as the non-recognition of transitional segments, but may be connected with the fact that the material originated from one locality only.

TABLE 12

THE NUMBER OF CAUDAL VERTEBRAE IN DIFFERENT SPECIES OF MACAQUES AND OF BABOONS

Species	Specimens	Average	Range
Macaca mulatta	92	16.6	13–20
Macaca nemestrinus	6	18.7	16–21
Macaca philippinensis	13	23.3	20–27
Macaca sinicus	4	24.3	23–25
Macaca irus	25	25.9	21–28
Papio sphinx	3	9.3	8–11
Papio papio	10	21.7	19–24

tons of *Hylobates concolor* the coccygeal vertebrae number only 1, 2, or 3 (average = 1.9), whereas all of the 6 specimens of *H. klossi* which could be examined have either 4 or 5 coccygeal segments (average = 4.5). The number of sacral vertebrae averages 3.5 in 11 specimens of *Papio hamadryas*, more than 3 vertebrae occurring in 6 cases, whereas among 15 specimens of *Papio papio* more than 3 sacral vertebrae have been found only twice and the average number equals 3.1. Finally, table 12 is inserted to record the numbers of caudal vertebrae in different species of macaques and of baboons, as found in specimens in which this number could be determined with certainty. These data supply ample support for the conclusion that different species of one and the same genus can at times differ significantly in regard to the number of vertebrae in one or another of the spinal regions. Such differences, however, usually have only limited diagnostic value in individual cases, since the ranges of variations in allied species rarely fail to overlap to some extent. Burmeister (1854) attempted to divide the capuchin monkeys into two main groups, the one containing species with 6 lumbar vertebrae and the other species with only 5 of these vertebrae. That this is an untenable proposal is evident from the fact that among 7 skeletons of *Cebus malitiosus*, examined by the writers, 3 have 6 lumbar vertebrae, 3 have 5, and the remaining one has only 4.

CONCLUSIONS AND SUMMARY

It is the chief purpose of this paper to supply accurate data, collected by strictly uniform methods, concerning the numbers of vertebrae in the various spinal regions in the different genera of primates. A total of 1457 specimens, representing 41 genera, have been examined. This material permits a comprehensive survey of the entire order Primates. Table 13 summarizes the results of this report in so far as the average numbers of vertebrae are concerned. This table includes a few figures, quoted from the literature for the sake of completeness, appertaining to the number of caudal segments in some of the rare genera for which no absolutely complete specimens have been available to the writers.

The number of cervical vertebrae, with rare

TABLE 13

AVERAGES OF THE NUMBERS OF VERTEBRAE OF THE VARIOUS SPINAL REGIONS IN THE DIFFERENT PRIMATE GENERA, ACCORDING TO THE FINDINGS OF THE PRESENT STUDY

The number of cervical vertebrae has been omitted, as it averages uniformly 7. * = quoted from Flower (1885), ** = quoted from Giebel and Leche (1874–1900) (records on single specimens).

Family	Genus	Average Number of Vertebrae				
		Thor.	Lumb.	Thor. + Lumb.	Sacr.	Caud.
Hypothetical Original Numbers		13	6	19	3	25
Daubentoniidae	Daubentonia	12.3	6.8	19.0	3.0	27*
Lemuridae	Lemur	12.1	6.7	18.9	2.9	27.0
	Myoxicebus	11.8	7.3	19.0	3.0	28.0
	Lepidolemur	12.0	9.3	21.3	3.7	21.5
	Microcebus	13.2	6.6	19.8	2.8	25.0?
	Chirogale	13.0	7.0	20.0	3.0	24*
	Lichanotus	12.0	8.0	20.0	3.5	23*
Lorisidae	Loris	14.7	8.3	23.0	4.5	5.0
	Nycticebus	16.1	7.1	23.2	6.1	7.0
	Perodicticus	15.3	6.2	21.5	6.1	10.9
	Galago	13.2	6.0	19.3	2.8	25.7
Tarsiidae	Tarsius	12.9	6.1	19.0	3.0	28.0
Hapalidae	Hapale	12.7	6.3	19.0	2.8	30.0
	Oedipomidas	12.4	6.6	19.0	3.0	32.0
	Leontocebus	12.0	7.0	19.0	2.7	33.0
Cebidae	Callicebus	12.0	7.5	19.5	3.0	25.5
	Aotus	13.9	7.1	21.0	3.0	26.0
	Pithecia	12.5	6.5	19.0	3.0	23.5
	Cacajao	13.0	6.0	19.0	4.0	17**
	Alouatta	14.1	5.1	19.2	3.2	27.3
	Saimiri	13.3	6.7	20.0	3.0	26.7
	Cebus	14.0	5.6	19.6	3.0	23.7
	Lagothrix	13.8	4.3	18.2	3.4	24.0
	Ateles	14.1	4.1	18.1	2.9	31.0
	Brachyteles	13.0	5.0	18.0	3.0	31**
Cercopithecidae	Macaca	12.2	6.9	19.0	3.0	19.1
	Cynopithecus	12.0	6.8	18.8	3.8	11.5
	Papio	12.5	6.5	19.0	3.2	19.7
	Theropithecus	12.5	6.5	19.0	3.0	26*
	Cercocebus	12.3	6.5	18.8	2.9	24.8
	Cercopithecus	12.2	6.9	19.0	3.1	26.4
	Erythrocebus	12.0	7.0	19.0	3.0	28*
	Semnopithecus	12.0	7.0	19.0	3.0	27.7
	Nasalis	12.1	6.9	19.0	3.1	24.6
	Colobus	12.0	6.8	18.8	3.0	26.0
Pongidae	Hylobates	13.1	5.1	18.2	4.6	2.7
	Symphalangus	12.8	4.5	17.4	4.7	2.4
	Pongo	11.9	4.0	15.9	5.4	2.6
	Pan	13.2	3.6	16.8	5.7	3.2
	Gorilla	12.9	3.7	16.6	5.7	3.0
Hominidae	Homo	12.0	5.0	16.9	5.3	3.8

individual exceptions, equals 7 in all primates. The exceptions are represented more often by decreases than by increases. The number of thoracic vertebrae fluctuates among primates between 11 and 18 in individual cases and between 12 and 16 as modal numbers for different genera. The lumbar vertebrae vary numerically between 2 and 10—the extremes being rare—and as modal numbers between 4 and 9. The combined number of thoracic and lumbar segments fluctuates individually between 15 and 24 and the generic modes of this number lie between 16 and 23. Among primates, anywhere from 2 to 8 vertebrae combine to form the sacrum, though the modal numbers range only between 3 and 6. The caudal region contains as many as 34 segments or, in other extreme cases, is not represented at all since the coccyx can be lacking completely. The range of the generic averages of the number of caudal vertebrae extends from 2.4 to 33.0.

The common ancestor of all primates in all likelihood possessed 7 cervical, 13 thoracic, 6 lumbar, 3 sacral, and about 25 caudal vertebrae. This original vertebral formula has become phylogenetically altered for one or several spinal regions and in various degrees in the great majority of the recent genera of primates, as shown by table 13. The number of thoracic segments has increased most of all in the prosimian subfamily Lorisinae, but also has become larger in some of the American monkeys, namely in the genera *Aotus*, *Alouatta*, *Cebus*, *Lagothrix*, and *Ateles*. Significant phylogenetic reductions in the number of thoracic segments have occurred in several lemuroid genera, in a few platyrrhine genera, in all catarrhine monkeys, in orang-utan, and in man. In all these forms, however, the modal number has decreased by only 1 segment. Evolutionary reductions in the number of thoracic vertebrae are not as great as are the increases, which equal as much as 3 segments in *Nycticebus*. The original number of 6 lumbar vertebrae has been retained as modal number by comparatively few primates. This number has become increased (to as much as 9) in the majority of the genera in the suborder Lemuroidea, and also has been added to significantly in some American and all Old World monkeys. Phylogenetic decreases in the number of lumbar segments are lacking in prosimians, but are characteristic of the platyrrhine genera *Alouatta*, *Lagothrix*, *Ateles*, and *Brachyteles*, and of all higher primates, having reached the extreme in the African great apes.

The number of thoracic + lumbar vertebrae, originally in all probability 19, has remained practically unchanged in *Daubentonia*, *Lemur*, *Myoxicebus*, *Galago*, and *Tarsius* among the prosimians and in the entire family Hapalidae, various genera of Cebidae, and all genera of Cercopithecidae among the simian primates. Evolutionary changes in the original number of thoracic + lumbar vertebrae involve only increases in the suborder Lemuroidea and are represented by both increases and decreases among the New World monkeys. In Old World simian primates only decreases in the number of thoracic + lumbar segments are encountered and these have occurred exclusively in the families Pongidae and Hominidae. This implies that the pelvis has shifted phylogenetically in a caudal direction or else remained stationary regarding the spinal column in the lower or prosimian primates and in the majority of the genera belonging to the platyrrhine series of simian primates. The only exception to this rule is found in the subfamily Atelinae of the latter series in which the pelvis has shifted one segment in a cephalic direction. In the catarrhine series of simian primates, finally, the pelvis has remained stationary in all the many different Old World monkeys and has migrated for at least one to at most three segments in a cephalic direction in the entire group of man-like apes and man. An increase in presacral segments is a wide-spread phenomenon among mammals, as has long ago been pointed out by Welcker (1881). On the other hand, an evolutionary reduction in the number of vertebrae between skull and pelvis represents a rare trend, limited to comparatively few and specialized types, namely, many bats, some American edentates, spider and woolly monkeys, anthropoid apes, and man. The number of sacral vertebrae has become very markedly increased by convergent evolutionary trends in two widely separated groups of primates—the Lorisinae and the higher primates.

The number of precaudal vertebrae is remarkably uniform in the great majority of primate genera. Most frequently this number averages 29. Only in the Atelinae and in the orang-utan has the modal number decreased to 28. Increases in this mode reach at most 31 in the suborder Simiae, but among the Lemuroidea the modal number for precaudal vertebrae frequently has become increased and this to as much as 36.

Phylogenetic trends towards additions to the

presumed original number of caudal segments are comparatively rare and not very pronounced among primates. Noteworthy increases have occurred only in a few prosimians, in the Hapalidae, in spider monkeys, and among guenons and langurs. In contrast to this, decreases in the number of tail segments are found to be frequent and far-reaching in lemuroid as well as in simian primates. Among the former the tail has become much reduced in number of segments in the indris and the Lorisinae. In platyrrhine monkeys the caudal region has undergone a reduction only in the uakari, but among catarrhine monkeys in many species of macaques, baboons and "black apes." The most extreme reductions are typical of all higher primates—the anthropoids and man.

An examination of table 13 reveals the fact that the vertebral formulae have undergone profound evolutionary changes affecting more than one spinal region in only two widely separate natural groups of primates, namely in the lemuroid subfamily Lorisinae and in the closely related simian familes Pongidae and Hominidae. The Lorisinae are characterized by the combination of vertebral additions to the thoracic, lumbar, and sacral regions with reductions in the caudal region. The man-like apes and man share the distinction of having greatly reduced numbers of lumbar and caudal vertebrae combined with an increased number of sacral vertebrae. The latter combination of changes has produced the lowest total numbers of vertebrae among primates. These totals average only 31 to 33 in man and anthropoids, whereas anywhere from 38 to 62 in all the remaining genera. In no respect has man attained the greatest extreme in these phylogenetic changes in the numbers of spinal segments; invariably he has been surpassed by one or another of the man-like apes.

Intragenerically, the individual combinations of numerical variations in the vertebrae of the different spinal regions do not occur in random fashion, but are limited in their distribution. It has been demonstrated that, as a rule, an increase in the number of segments in one spinal region either is accompanied by a decrease in the number of segments in the adjoining region or else leaves the latter number unaffected; but a plus variation in one region does not combine with a plus variation in the next region. In accordance, a spinal region may lose a segment to the gain of the adjoining region or without affecting the latter, but such a loss in one region is not associated with a loss in the neighboring region. Variations in the number of thoracic vertebrae influence the number of lumbar vertebrae much more frequently than they do the number of cervical vertebrae and, hence, the thoraco-lumbar border is less stable than the cervico-thoracic border. Vertebral transformations at the lumbo-sacral border are somewhat less common than those at the sacro-caudal border.

The tendency to deviate individually from the modal number of vertebrae differs very widely in the various spinal regions as well as in the various primate genera. The number of cervical vertebrae is extremely stable. The numbers of thoracic, of lumbar, and of sacral vertebrae show, on an average, rather high and very similar degrees of variability. The number of caudal vertebrae is far more variable than are the numbers of vertebrae in the precaudal spinal regions. Among the different primate genera, numerical variations of vertebrae are most common in pottos and rarest in langurs. Man is much more stable in this respect than are the man-like apes, but somewhat less stable than most catarrhine monkeys, particularly the Semnopithecinae.

The existence of definite hereditary trends for the occurrence of vertebral variations has been conclusively demonstrated by a number of recent investigators, notably by Kühne (1931, 1936) and by Frede (1934). It is not surprising, therefore, to find that species of the same genus can at times differ significantly in regard to the average number of vertebrae in one or another spinal region. Among primates such species differences are most common and pronounced in the caudal region. As has already been fully discussed by Fischer (1933), the hereditary nature of segmental variations within species forms the basis for the phylogenetic trends which have differentiated the vertebral formulae among recent primates.

REFERENCES

ABEL, O. 1931. Die Stellung des Menschen im Rahmen der Wirbeltiere. Jena.

ALLEN, J. A. 1925. Primates collected by the American Museum Congo expedition. *Bull. Amer. Mus. Nat. Hist.* **47**: 283–499.

BURMEISTER, H. 1854. Ueber die Arten der Gattung Cebus. *Abh. Naturf. Ges. Halle*, 2. H.

CLARK, W. E. LE G. 1926. On the anatomy of the pentailed tree-shrew (Ptilocercus lowii). *Proc. Zool. Soc. London*, 1179–1309.

—— 1934. Early forerunners of man. London.

DAVIS, D. D. 1938. Notes on the anatomy of the treeshrew Dendrogale. *Zool. Ser. Field Mus. Nat. Hist.* **20**: 383–404.

ELLIOT, D. G. 1913. A review of the primates. 3 v. Amer. Mus. Nat. Hist., Monograph I.

FICK, R. 1933. Untersuchungen an der Wirbelsäule der Menschenaffen. *Sitzber. Preuss. Akad. Wiss., Phys.-Math. Kl.*, 167–239.

—— 1936. Untersuchungen an der Wirbelsäule von 30 Gibbons und über die Wirbelzahlen der Menschenaffen. *Sitzber. Preuss. Akad. Wiss., Phys.-Math. Kl.*, 161–178.

FISCHER, E. 1933. Genetik und Stammesgeschichte der menschlichen Wirbelsäule. *Biol. Zentralbl.* **53**: 203–220.

FLOWER, W. H. 1862. Notes on the anatomy of Pithecia monachus (Geoff.). *Proc. Zool. Soc. London*, 326–333.

—— 1884. Catalogue of the specimens illustrating the osteology and dentition of vertebrated animals, recent and extinct, contained in the Museum of the Royal College of Surgeons of England. Part II, Mammalia. London.

—— 1885. An introduction to the osteology of the Mammalia. 3rd ed. revised with the assistance of H. Gadow. London.

FREDE, M. 1934. Untersuchungen an der Wirbelsäule und den Extremitätenplexus der Ratte. *Zschr. Morphol. Anthropol.* **33**: 96–150.

GADOW, H. F. 1933. The evolution of the vertebral column. Cambridge, Eng.

GIEBEL, C. G., AND W. LECHE. 1874–1900. Säugethiere: Mammalia. *Bronn's Klassen u. Ordnungend es Thier-Reichs*, **6** (5).

GREGORY, W. K. 1913. Relationship of the Tupaiidae and of the Eocene lemurs, especially Notharctus. *Bull. Geol. Soc. Amer.* **24**: 247–252.

—— 1916. Studies on the evolution of the primates. *Bull. Amer. Mus. Nat. Hist.* **35**: 239–355.

—— 1920. On the structure and relations of Notharctus, an American Eocene primate. *Mem. Amer. Mus. Nat. Hist.*, n.s. **3**: 47–243.

HRDLIČKA, A. 1916. Physical anthropology of the Lenape or Delawares, and of the eastern Indians in general. *Bureau Amer. Ethnol.*, Bull. **62**.

JENTINK, F. A. 1885. On some rare and interesting mammals. *Notes Leyden Museum* **7**: 37 (quoted by Lyon, 1913).

KEITH, A. 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. *Jour. Anat. Physiol.* **37**: 18–40.

KOHLBRÜGGE, J. H. F. 1891. Versuch einer Anatomie des Genus Hylobates. *Zool. Ergeb. einer Reise in Niederländ. Ost-Indien*, I, 211–354. Leiden.

KÜHNE, K. 1931. Die Vererbung der Variationen der menschlichen Wirbelsäule. *Zschr. Morphol. Anthropol.* **30**: 1–221.

—— 1936. Die Zwillingswirbelsäule (eine erbgenetische Forschung). *Zschr. Morphol. Anthropol.* **35**: 1–376.

LE DOUBLE, A. F. 1912. Traité des variations de la colonne vertébrale de l'homme. Paris.

LYON, N. W., JR. 1913. Treeshrews: An account of the mammalian family Tupaiidae. *Proc. U. S. Nat. Mus.* **45**: 1–188.

MILLER, G. S., JR. 1933. The classification of the gibbons. *Jour. Mammal.* **14**: 158–159.

MIVART, ST. G. 1865. Contributions towards a more complete knowledge of the axial skeleton in the primates. *Proc. Zool. Soc. London*, 545–592.

NAYAK, U. V. 1933. Note on an unusual type of cervical rib in a lemur. *Jour. Anat.* **68**: 119–121.

POCOCK, R. J. 1907. A monographic revision of the monkeys of the genus Cercopithecus. *Proc. Zool. Soc. London*, 677–746.

—— 1926. The external characters of the catarrhine monkeys and apes. *Proc. Zool. Soc. London* 1925: 1479–1585.

RANDALL, F. E. 1943–1944. The skeletal and dental development and variability of the gorilla. *Human Biol.* **15**: 236–254, 307–337; **16**: 23–76.

ROSENBERG, E. 1876. Ueber die Entwicklung der Wirbelsäule und das Centrale carpi des Menschen. *Morphol. Jahrb.* **1**: 83–197.

SCHULTZ, A. H. 1930. The skeleton of the trunk and limbs of higher primates. *Human Biol.* **2**: 303–438.

—— 1932. The generic position of Symphalangus klossii. *Jour. Mammal.* **13**: 368–369.

—— 1933. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs. *Human Biol.* **5**: 212–255, 385–428.

—— 1934. Some distinguishing characters of the mountain gorilla. *Jour. Mammal.* **15**: 51–61.

—— 1938. The relative length of the regions of the spinal column in Old World primates. *Amer. Jour. Phys. Anthropol.* **24**: 1–22.

—— 1940. Growth and development of the chimpanzee. *Contrib. to Embryol.* **28**, *Carnegie Inst. Wash. Publ.* 518, 1–63.

—— 1941. Growth and development of the orang-utan. *Contrib. to Embryol.* **29**, *Carnegie Inst. Wash. Publ.* 525, 57–110.

—— 1942. Growth and development of the proboscis monkey. *Bull. Mus. Comp. Zool.* **89**: 277–314.

—— 1944. Age changes and variability in gibbons. *Amer. Jour. Phys. Anthropol.*, n.s. **2**: 1–129.

SIMPSON, G. G. 1931. A new classification of mammals. *Bull. Amer. Mus. Nat. Hist.* **59**: 259–293.

SONNTAG, C. F. 1924. The morphology and evolution of the apes and man. London.

SPERANSKY, A. D. 1926. Ueber die lumbosakrale Abteilung der Primaten Wirbelsäule. *Zschr. Anat. Entw. Gesch.* **78**: 111–135.

STRUTHERS, J. 1893. On the articular processes of the vertebrae in the gorilla compared with those in man, and on costo-vertebral variation in the gorilla. *Jour. Anat. Physiol.* **27**: 131–138.

TODD, T. W. 1922. Numerical significance in the thoracicolumbar vertebrae of the Mammalia. *Anat. Rec.* **24**: 261–286.

WEBER, M. 1927–1928. Die Säugetiere. 2nd ed., Jena.

WELCKER, H. 1881. Die neue anatomische Anstalt zu Halle durch einen Vortrag über Wirbelsäule und Becken. *Arch. Anat. Physiol., Anat. Abth.*, 161–192.

ZUCKERMAN, S. 1938. Observations on the autonomic nervous system and on vertebral and neural segmentation in monkeys. *Trans. Zool. Soc. London* **23**: 315–378.

INDEX TO VOLUME 89

American Philosophical Society and the early history of forestry in America (Chinard), 444
Antarctic Service Expedition, 1939–1941, Scientific results of, 1
Appel, Anita, with B. O. Dodge, see Dodge
Arabic bilingual entagion (Bell), 531
Areopagitica—1644 (Osgood), 495

Bailey, Dana K., with S. A. Korff, see Korff
Bartsch, Paul, Mollusks of the U. S. Antarctic Service Expedition, 1939–1941, 294
Bell, Harold Idris, The Arabic bilingual entagion, 531
Berlin, Leonard M., Ground surveys accomplished at West Base, Antarctica, 386
Binary systems, close, Theoretical velocity curves of (Kopal), 517
Black, John D., The role of federal, state, and local governments in promoting forestry, 434
Black, Richard B., Geographical operations from East Base, U. S. Antarctic Service Expedition, 1939–1941, 4
Blakeslee, Albert F., Removing some of the barriers to crossability in plants, 561
Boyd, Vernon D., Motorized surface transportation in the Antarctic, 379
Bryant, Herwil M., Biology at East Base, Palmer Peninsula, Antarctica, 256
Byrd, Richard E., Preface to reports on scientific results of the U. S. Antarctic Service Expedition, 1939–1941, iii
  Exploratory flights of (1940) (Hawthorne), 398a

Calcium, Plasma, in birds and mammals (Riddle and Dotti), 499
Chinard, Gilbert, The American Philosophical Society and the early history of forestry in America, 444
Clark, Austin H., Echinoderms of the U. S. Antarctic Service Expedition, 1939–1941, 295
Clarke, Eric T., with S. A. Korff, see Korff
Colonial theory, English, Sir Thomas Smith (1513–1577) and the beginnings of (Quinn), 543
Compton, Wilson, Forest conservation; a task in engineering and in public and private cooperation, 423
Court, Arnold, Field altitudes of West Base parties U. S. Antarctic Service Expedition, 1939–1941, 61
  Weather observations during 1940–1941 at Little America III, Antarctica, 324
Crossability in plants, Removing some of the barriers to (Blakeslee), 561
Cushman, Joseph A., Foraminifera of the U. S. Antarctic Service Expedition, 1939–1941, 285

Deichmann, Elisabeth, An octocoral of the U. S. Antarctic Service Expedition, 1939–1941, 294
Dodge, B. O., Mary B. Schmitt, and Anita Appel, Inheritance of factors involved in one type of heterocaryotic vigor, 575
Dorsey, H. G., Jr., An Antarctic mountain weather station, 344
Dotti, Louis B., with Oscar Riddle, see Riddle

East Base, Palmer Peninsula, U. S. Antarctic Service Expedition, 1939–1941, Geographical operations from (Black), 4
  An Antarctic mountain weather station (Dorsey), 344
  Biology at (Bryant), 256
  Condensed ornithology report (Eklund), 299
  Geology of Southern Palmer Peninsula, Antarctica (Knowles), 132
  Glaciology of Southern Palmer Peninsula, Antarctica (Knowles), 174
  Main southern sledge journey from (Ronne), 13
Eclipses, atmospheric, An outline of the theory of (Kopal), 590
Eklund, Carl R., Condensed ornithology report, East Base, Palmer Land, 299
Entagion, The Arabic bilingual (Bell), 531
Essential human rights, Statement of, by representatives of the principal cultures of the world (Lewis), 489
Ewing, H. E., Mites of the U. S. Antarctic Service Expedition, 1939–1941, 296

Forestry and the public welfare, symposium, 399
Frazier, Russell G., Acclimatization and effects of cold on the human body as observed at Little America III, on the U. S. Antarctic Service Expedition, 1939–1941, 249
Friedmann, Herbert, Birds of the U. S. Antarctic Service Expedition, 1939–1941, 305
  Pelagic birds from the west coast of South America, 314

Glance, Grace, Collembola of the U. S. Antarctic Service Expedition, 1939–1941, 295

Hawthorne, Roger, Exploratory flights of Admiral Byrd (1940), 398a
Heterocaryotic vigor, Inheritance of factors involved in one type of (Dodge, Schmitt, and Appel), 575
Hormones, Pituitary and sex, which increase plasma calcium in birds and mammals (Riddle and Dotti), 499
Human rights, Statement by representatives of the principal cultures of the world (Lewis), 489

Kaylor, Joseph F., Public control of cutting practices on private timberlands, 428
Knowles, Paul H., Geology of southern Palmer Peninsula, Antarctica, 132
  Glaciology of southern Palmer Peninsula, Antarctica, 174
Kopal, Zdeněk, Theoretical velocity curves of close binary systems, 517
  An outline of the theory of atmospheric eclipses, 590
Korff, S. A., Dana K. Bailey, and Eric T. Clarke, Report on cosmic-ray observations made on the U. S. Antarctic Service Expedition, 1939–1941, 316
Kotok, E. I. America's role in meeting world timber needs, 418

Lewis, William Draper, The statement of essential human rights by representatives of the principal cultures of the world, 489

Little America III, see West Base
Lockhart, Ernest E., Antarctic trail diet, 235
Lowdermilk, W. C., World-wide needs of woods as a land conservation crop, 408

McCoy, James C., Report on aircraft activities at West Base, Antarctica, 387

Osgood, Charles G., *Areopagitica*—1644, 495

Palmer Peninsula, see East Base
Passel, Charles F., Sedimentary rocks of the southern Edsel Ford Ranges, Marie Byrd Land, Antarctica, 123
with Paul A. Siple, see Siple
Perkins, Jack E., Biology at Little America III, the West Base of the U. S. Antarctic Service Expedition, 1939–1941, 270
Plants, Removing some of the barriers to crossability in (Blakeslee), 561
Primates, The numbers of vertebrae in (Schultz and Straus), 601
Public welfare, Forestry and, symposium, 399

Quinn, David B., Sir Thomas Smith (1513–1577) and the beginnings of English colonial theory, 543

Riddle, Oscar, and Louis B. Dotti, Pituitary and sex hormones which increase plasma calcium in birds and mammals, 499
Ronne, Finn, The main southern sledge journey from East Base, Palmer Land, Antarctica, 13

Schmitt, Mary B., with B. O. Dodge, see Dodge
Schmitt, Waldo L., Miscellaneous zoological material collected by the U. S. Antarctic Service Expedition, 1939–1941, 297
Schultz, Adolph H., and William L. Straus, Jr., The numbers of vertebrae in primates, 601
Schultz, Leonard P., Fishes of the U. S. Antarctic Service Expedition, 1939–1941, 298
Shirley, Charles C., Photographic accomplishments and phogographic technique of West Base, Antarctica, 382
Shoemaker, Clarence R., Amphipoda of the U. S. Antarctic Service Expedition, 1939–1941, 289
Siple, Paul A., Geographical exploration from Little America III, the West Base of the U. S. Antarctic Service Expedition, 1939–1941, 23
General principles governing selection of clothing for cold climates, 200
and Charles F. Passel, Measurements of dry atmospheric cooling in subfreezing temperatures, 177
Smith, Sir Thomas (1513–1577), and the beginnings of English colonial theory (Quinn), 543
Stewart, Duncan, Jr., Preliminary report on some intrusives of the Melchior Islands, Antarctica, 146
Abstracts of works on Antarctic petrography, 152
The petrography of some intrusive rocks from King Edward VII and Marie Byrd Lands, Antarctica, 148
Straus, William L., Jr., with Adolph H. Schultz, see Schultz
Symposia:
Forestry and the public welfare, 399
Reports on scientific results of the U. S. Antarctic Service Expedition, 1939–1941, 1

Timber, timberlands, see forestry

U. S. Antarctic Service Expedition, 1939–1941, Scientific results of, 1

Vertebrae in primates, The numbers of (Schultz and Straus), 601

Wade, F. Alton, An introduction to the symposium on scientific results of the U. S. Antarctic Service Expedition, 1939–1941, 1
The geology of the Rockefeller Mountains, King Edward VII Land, Antarctica, 67
The physical aspects of the Ross Shelf Ice, 160
Warner, Lawrence A., Structure and petrography of the southern Edsel Ford Ranges, Antarctica, 78
West Base, Little America III, U. S. Antarctic Service Expedition, 1939–1941, Geographical exploration from (Siple), 23
Biology (Perkins), 270
Field altitudes of parties (Court), 61
Geology of the Rockefeller Mountains, King Edward VII Land (Wade), 67
Ground surveys accomplished (Berlin), 386
Petrography of some intrusive rocks from King Edward VII and Marie Byrd Lands (Stewart), 148
Photographic accomplishments and photographic technique (Shirley), 382
Report on aircraft activities (McCoy), 387
Results of auroral observations, April–September 1940 (Wiener), 364
Sedimentary rocks of the southern Edsel Ford Ranges (Passel), 123
Structure and petrography of southern Edsel Ford Ranges (Warner), 78
Weather observations during 1940–1941 (Court), 324
Wiener, Murray A., Results of auroral observations at West Base, Antarctica, April to September, 1940, 364
Winslow, Carlile P., Wood in the national economy, 403
Wood, woods, see forestry

Zon, Raphael, Forests in relation to soil and water, 399

EXPLORATORY FLIGHTS OF ADMIRAL BYRD (1940) *

ROGER HAWTHORNE

Recorder, U. S. Antarctic Service

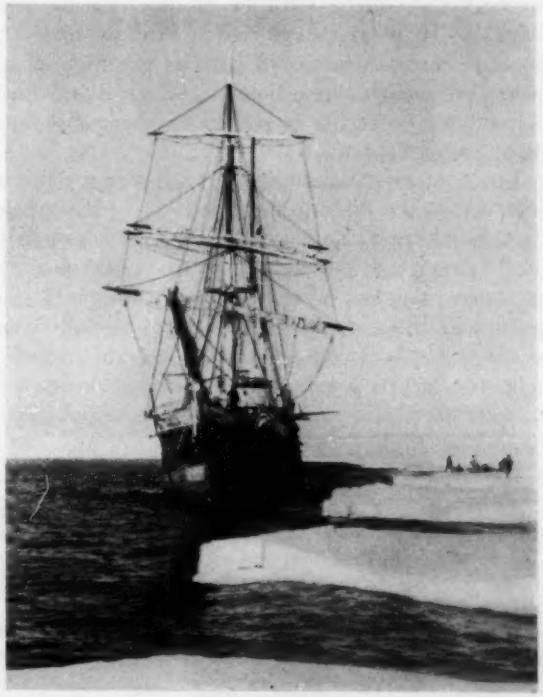
THREE exploratory cruises of the plane-equipped U.S.S. *Bear*, flagship of the United States Antarctic Service in 1940, resulted in discovery by Rear Admiral Richard E. Byrd, U.S.N. (Ret.),[1] of approximately 800 miles of heretofore uncharted coastline and exploration by sea and air of more than 100,000 square miles of unknown regions east of Little America III. For convenience, the separate undertakings are identified as (1) the Eastern Exploratory Cruise, (2) the South Magnetic Pole Exploratory Cruise, and (3) the Pacific Quadrant Exploratory Cruise.

THE EASTERN EXPLORATORY CRUISE

The Eastern Cruise was undertaken by U.S.S. *Bear* under the command of Lieutenant Commander R. H. Cruzen, U.S.N., on January 19, 1940, five days after her rendezvous with U.S.M.S. *North Star* at the Bay of Whales. Admiral Byrd, the Commanding Officer of the expedition; ten members of the East Base Ice Party, and the entire personnel of the *Bear* participated in this and the two subsequent cruises.

The primary purpose of the Eastern Exploratory Cruise was the discovery and delineation of unexplored coastline east of the 148th meridian.[2] This suggested the advisability of a visit to the vicinity of Cape Colbeck to determine whether a thrust to the eastward close to the coast of Marie Byrd Land might not be made possible by a late seasonal movement of bay ice northward from the edge of the Continent. The Commanding Officer who had been prevented by heavy pack ice and unfavorable flying conditions on two previous expeditions from reaching Marie Byrd Land from the north,[3] had long believed that open water might be found close to the coast by any ship thrusting eastward from the Bay of Whales late in the season.

Conditions encountered at Cape Colbeck on January 22 appeared to support this theory and on January 25 the *Bear* navigated through the ice



Official U. S. Antarctic Service photo

FIG. 1. U.S.S. *Bear* departing Bay of Whales for Palmer Land and East Base.

* Because of unforeseen circumstances this article was not available in time to be incorporated with the other papers issued in the number of the *Proceedings* entitled "Reports on Scientific Results of the United States Antarctic Service Expedition, 1939–1941." It is issued here so that it may be bound at the appropriate place in the volume. Due to Admiral Byrd's absence from the country, he did not see the article before it went to press but the author has taken every possible step to substantiate the material. ED.

[1] The data used in this paper are based upon notes and log entries made in the field by the Recorder. Owing to wartime conditions and oversea assignments of expedition personnel, including Rear Admiral Richard E. Byrd, it has been impossible to confirm, prior to publication, all given positions of latitude and longitude. Fixed positions are given when available and dead-reckoned positions only in the absence of corrected coordinates. It is not intended that positions given herein be accepted as completely authoritative although they were officially logged in the field and may be presumed to be authoritative.

[2] By direction of President Franklin D. Roosevelt, late in 1939.

[3] 1928–1930 and 1933–1935.

Official U. S. Antarctic Service photo

FIG. 2. Admiral Byrd standing on wing of Barkley-Grow after flight attempt on Eastern Exploratory Cruise.

pack to 74° 43′ S., 143° 52′ 30″ W.,[4] or approximately 125 miles farther east at that latitude than any previous vessel in the history of Antarctic exploration. The Commanding Officer attributed the success of this venture to the extremely valuable assistance of the twin-motored Barkley-Grow seaplane which made four important reconnaissance flights in the face of unfavorable weather conditions and an equal number of shorter flights in search of navigable leads through heavy pack.[5]

The first of the four major flights made in this area was taken on January 22, 1940.[6] It revealed that Sulzberger Bay was much more extensive than previously believed and confirmed the presence of a large bay ten miles long and five miles wide previously sighted from the ship east of Cape Colbeck on January 19. Its eastward cape, formed by a grounded tabular iceberg three miles long, was linked with the mainland by shelf ice. The flight also disclosed a 50-mile wide strip of open water to the northeast which permitted the *Bear* to advance to 76° 39′ S., 154° W.

The following day, January 23, a second flight disclosed that Jacob Ruppert Coast extended at least 40 miles farther than previously believed and revealed another ice-locked sea almost 100 miles wide far east of the *Bear*'s position. Leads were spotted from the air and on January 25 the ship moored to shelf ice at 74° 43′ S., 143° 52′ 30″ W.,[7] the most eastern and southern point ever reached by any ship in this area.[8]

On the January 23 flight, the plane party was hampered by poor visibility in the vicinity of the Chester Mountains but, turning in a northeasterly direction toward the coast, reached 75° 30′ S., 147° 30′ W., where coastline could be seen extending between 20 and 30 miles farther in an easterly direction.

Violent gales delayed further air operations until January 25 when a new mountain range was believed sighted from the plane but its position was not verified until the following day, January 26, when only a few minutes after the take-off mountain peaks were clearly seen to the eastward. This range extended in an easterly direc-

U. S. Antarctic Service photo, courtesy of H. G. Dorsey, Jr.

FIG. 3. Mount Melbourne from the southeast, Terra Nova Bay, South Victoria Land. At the right is the craggy headland of Cape Washington.

[4] *Cf.* Siple, P. A., Geographical exploration from Little America III, *Proc. Amer. Philos. Soc.* **89**: 39, 1945.

Cf. English, R. A. J., Preliminary account of the United States Antarctic Expedition, 1939–41, *Geog. Rev.* **31**: 467, 1941.

[5] The Barkley-Grow seaplane was piloted by Ashley C. Snow, Aviation Chief Machinist's Mate (N.A.P.) and Earl B. Perce, Radioman First Class (N.A.P.), assistant pilot. Admiral Byrd was observer-navigator. On several short flights Captain Cruzen and Captain Bendik Johansen (sailing master) were taken aloft as observers.

[6] *Cf.* English, R. A. J., *op. cit.* English's statement that this flight was made on January 21 appears to be erroneous. The flight on January 21 was a short, radio compass calibration flight. The flight over Sulzberger Bay was made the following day.

[7] See footnote 4.

[8] Few Antarctic explorers ever have even approached this region. Cook reached the 67th parallel in 1773, Charcot the 70th in 1910, and Sir Hubert Wilkins, far to the eastward, penetrated to latitude 73° S., in 1930.

Official U. S. Antarctic Service photo

FIG. 4. Admiral Byrd operating dip needle at Drygalski Ice Tongue.

tion for approximately 120 miles and from that point additional masses could be seen extending 70 or 80 miles to the south. One of the mountains, approximately 4000 feet high, with its summit lost in the clouds, appeared to be 40 miles long. On the return flight the Barkley-Grow also passed over, close to the coast, a partially exposed island 200 to 300 feet high.[9]

Worsening weather, unfavorable ice conditions, and lateness of the season indicated a necessity for immediate withdrawal. With some difficulty the *Bear* worked free of the ice pack and on January 30 returned to the Bay of Whales.

THE SOUTH MAGNETIC POLE CRUISE

It appeared unwise to attack the Antarctic Coast east of the 130th meridian in the earlier part of February, so it was decided to spend a week investigating the South Magnetic Pole area. The *Bear* therefore left the Bay of Whales for the last time on February 1 and laid a course for South Victoria Land.

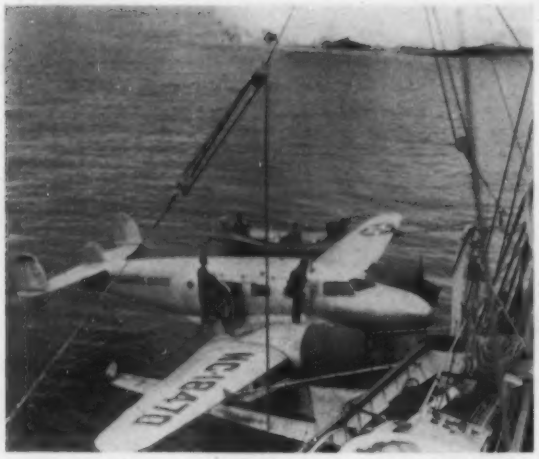
Several mountains, an island, and long Barrier tongues believed not to have been previously reported were charted and the coast was explored for 180 miles, but because of bad ice conditions in Wood Bay and elsewhere along the coast northward to Coulman Island it was impossible to moor the ship. Terra Nova Bay proved to be navigable but the Barrier was too high to land a shore party and the only suitable mooring found on the entire coast was alongside Drygalski Ice Tongue at 75° 10′ 30″ S., 163° 37′ 30″ E.

All plans for a flight to the Magnetic Pole had to be abandoned because of strong, variable winds and sastrugi. A working party attempted to smooth out an airstrip but changeable winds indicated that a take-off would be hazardous in the extreme. Pontoons were available for a sea take-off but were considered too heavy for the high altitude of the Magnetic Pole Plateau.

Dip circle observations were taken from the surface of Drygalski Ice Tongue and a line of bearing established from a point approximately 195 miles from the Pole.[10] The results were not conclusive but it was noted with interest that the bearing line passed between positions charted by Professor David in 1909 and Sir Douglas Mawson in 1912. Although the Pole appeared to lie a few miles east of the position plotted by Mawson, it lay west of three other positions suggested by terrestrial magnetists and appeared to

[9] English places this at about 74° 30′ S., 141° W. *Op. cit.*

[10] The Magnetic Pole.



Official U. S. Antarctic Service photo

FIG. 5. Hoisting seaplane aboard U.S.S. *Bear*.

lie about 30 miles west of the position reported by David.

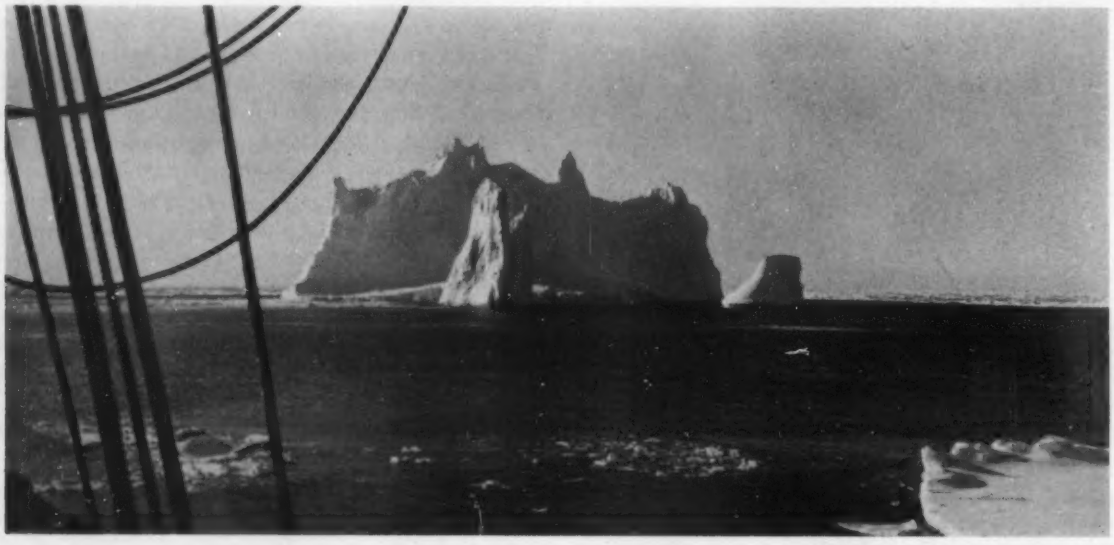
THE PACIFIC QUADRANT CRUISE

The primary objective of the U. S. Antarctic Service was the discovery and delineation of coastline between longitude 80° W. and 148° W., or the Pacific Quadrant. More than 300 miles of the 1,400 miles of unknown coastline in that area had been charted during the Eastern Exploratory Cruise in January but it was felt that the expedition's major objective would not be accomplished without discovery of a substantial part of the coastline between Marie Byrd Land and Alexander Island. It was toward this coast that the *Bear* turned after leaving South Victoria Land on February 7.

Fog, increasing darkness, high seas, and numerous icebergs made flight operations impossible until February 19. During this time the *Bear* remained as close to the pack as was consistent with safety, charting its contours and penetrating leads wherever the opportunity offered. The *Bear* sailed, in general, a more southerly route than that of the S.S. *Jacob Ruppert* in 1933–1934 and passed the *Ruppert*'s southernmost position on February 19 at 70° 04′ S., 116° 03′ W. On the same date, Lieutenant George J. Dufek, U.S.N., navigator of the *Bear*, Snow, and Perce made a brief flight. Clear water was seen ahead but bad weather and high seas prevented further reconnaissance until February 24.

Two attempted take-offs from the lee of tabular icebergs failed but at 12:58 P.M. (LAT) the Commanding Officer, Snow, and Perce flew 190 miles due south from the *Bear*'s position at 70° 44′ S., 108° 26′ W.[11] It was this flight which resulted in the discovery of the area now tentatively designated as Franklin Roosevelt Sea and Walgreen Coast. Land was sighted dead ahead of the plane and from an altitude of 5,500 feet the flight crew saw two mountain ranges beyond which lay an elevated snow-covered plateau. The ranges,

[11] English places the *Bear*'s position at 70° 43′ S., 108° 25′ W. *Op. cit.*



Official U. S. Antarctic Service photo

FIG. 6. Berg passed by U.S.S. *Bear* en route to Palmer Peninsula.

which appeared to be about 7,500 feet high, extended for about 100 miles in an east-west direction.[12] Eighty miles off the coast and approximately 110 miles from the *Bear*'s position the flight crew also sighted an island five or six miles long, covered with ice and snow. About 200 miles of the new coastline, the goal of explorers since the late eighteenth century, were photographed and charted before the plane retraced its course and landed alongside the *Bear* at 4:10 P.M. (LAT).

During the night the *Bear* steamed eastward and the following day, February 25, Dufek, Snow, and Perce took off from 70° 58′ S., 105° 47′ W.[13] After flying south for 50 miles, land was sighted in a southeasterly direction and within a half-hour the plane was abreast two parallel mountain ranges about 3,500 or 4,000 feet high. The mountains, apparently identical with those reported the previous day by Admiral Byrd, also were described by Dufek as running in an east-west direction and as defining the limits of an elevated plateau. After charting 100 miles of coastline Dufek turned back.

The third and most successful of the three flights in this area was made February 27 after the *Bear* had skirted the ice pack in an easterly direction to 70° 04′ 30″ S., 95° 19′ W. The Commanding Officer's discovery of a great, mountainous peninsula, a huge, ice-filled bay, and two large islands brought the total length of newly charted coastline to approximately 800 miles and increased the total of explored territory to more than 100,000 square miles.

[12] English says this mountain range trended in an east-west direction about 10 miles farther south. *Op. cit.* Presumably this is a typographical error. On returning from his flight Admiral Byrd placed it at about 100 miles.

[13] English places the *Bear*'s position at 70° 58′ S., 105° 33′ W. *Op. cit.*

Official U. S. Antarctic Service photo

FIG. 7. Heavy ice pack on the way to East Base.

On this last flight mountain ranges were discovered to the westward only 40 minutes after the Barkley-Grow took off. The peninsula of which they formed a part extended from the Continent more than 100 miles to approximately 72° 45′ S. The peaks ranged in height from 2,000 to 3,000 feet and one mountain about 4,000 feet high was clearly visible to the southeast in the vicinity of the 96th meridian. The peninsula's western shore formed an enormous bay scored with numerous ice-choked coves and inlets while just offshore, lying at approximately 71° 50′ S., 96° W., were two large islands. Inland, high terrain and what appeared to be great snow-covered ridges swept eastward to approximately the 88th meridian.

The return flight was made safely but the wind increased to gale force and no further flights were possible in this area. The *Bear* continued toward Palmer Peninsula to participate in the establishment of East Base.

PUBLICATIONS

OF

The American Philosophical Society

The publications of the American Philosophical Society consist of PROCEEDINGS, TRANSACTIONS, MEMOIRS, and YEAR BOOK.

The PROCEEDINGS contains original papers which have been read before the Society in addition to other papers which have been accepted for publication by the Committee on Publications. Beginning with Volume 88 one volume is issued each year and the price is $5.00 net per volume.

The TRANSACTIONS, the oldest scientific journal in America, was started in 1769; its quarto size makes it especially suitable for the publication of treatises and monographs requiring large illustrations. Beginning with Volume 34 one volume is issued each year and the price is $6.00 net per volume. The annual subscription price for both the PROCEEDINGS and the TRANSACTIONS is $10.00.

Each volume of the MEMOIRS is published in book form. The titles cover a variety of subjects. The price of each volume is determined by its size and character; the prices have varied from $1.50 to $7.50.

The YEAR BOOK is of considerable interest to scholars because of the reports on grants for research and also because of the section devoted to the Library which contains in greater or less detail description of important holdings and accessions. In addition it contains the Charter and Laws, and lists of Officers, Committees, and Members. The YEAR BOOK is published as soon as possible after the close of each calendar year. The price is $1.50.

A catalogue of the contents of the publications may be had
by addressing the

AMERICAN PHILOSOPHICAL SOCIETY

INDEPENDENCE SQUARE

PHILADELPHIA 6, PA.

THE AMERICAN PHILOSOPHICAL SOCIETY

Recent Publications

PROCEEDINGS: (The following are symposia.)

The Early History of Science and Learning in America.
Vol. 86, no. 1, 204 pp., 25 fig., 1942; Vol. 87, no. 1, 119 pp., 55 fig., 1943. $1.25 each.

Post-War Problems.
Vol. 87, no. 2, 78 pp., 4 fig., 1943. $1.00.

Thomas Jefferson.
Vol. 87, no. 3, 91 pp., 7 pl., 1943. $1.00.

The Organization, Direction, and Support of Research.
Vol. 87, no. 4, 74 pp., 1944. $.75.

Taxation and the Social Structure.
Vol. 88, no. 1, 67 pp., 1944. $1.00.

Wartime Advances in Medicine.
Vol. 88, no. 3, 69 pp., 6 fig., 1944. $1.00.

Reports on Scientific Results of the United States Antarctic Service Expedition, 1939-1941.
Vol. 89, no. 1, 398 + vi pp., 321 fig., 10 maps, 1945. $4.00.

Forestry and the Public Welfare.
Vol. 89, no. 2, 90 pp., 11 fig., 1945. $1.00.

TRANSACTIONS:

The Velocity of Light, by N. Ernest Dorsey.
Vol. 34, pt. 1, 110 pp., 20 fig., 1944. $2.25.

The Arc Spectrum of Iron (Fe I), by Henry Norris Russell, Charlotte E. Moore, and Dorothy W. Weeks.
Vol. 34, pt. 2, 97 pp., 1944. $2.25.

The Mammalia of the Duchesne River Oligocene, by William B. Scott.
Vol. 34, pt. 3, 45 pp., 8 pl., 1945. $2.25.

Purveyance for the Royal Household in the Reign of Queen Elizabeth, by Allegra Woodworth.
Vol. 35, pt. 1, 89 pp., 1945. $1.25.

MEMOIRS:

Sumerian Mythology: A Study of Spiritual and Literary Achievement in the Third Millennium B. C., by S. N. Kramer.
Vol. 21, 125 pp., 21 pl., 3 fig., 1944. $2.00.

Thomas Jefferson's Garden Book, annotated by Edwin M. Betts.
Vol. 22, 704 pp., 37 pls., 1944. $5.00.